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Information Acquisition and Communication and its Impact on Social Structure

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Declaration

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Abstract

Aggregation into groups is common in many species in the animal kingdom. Pressures on individuals to aggregate range from predation avoidance to thermo-regulation. The information centre hypothesis proposes that information sharing was the main pressure in the evolution of colonial social structures. We build an agent-based model to explore how variations in the environment affect how individuals within a colony acquire information. Our model shows that as resources become more patchily distributed and more ephemeral, social acquisition of information becomes more beneficial. These results show under what circumstances the ability to acquire information socially may benefit those in aggregate social structures. However, further work needs to be done in order to explain the information centre hypothesis' main point of contention, the motivation for successful foragers to return to the colony.

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Part I

Introduction and Background Information

Chapter 1

Introduction

Numerous social structures exist in the animal kingdom, all of which have evolved to fill a niche in the environment in which the organisms find themselves. The various levels of aggregation and hierarchy within the majority of these social structures can be explained by selective pressures such as predation avoidance, resource exploitation and mating opportunity. In some situations, however, these pressures fail to explain observed patterns of behaviour. The possibility of acquiring social and ecological information is thought to be a benefit of aggregation. The information centre hypothesis proposes that this benefit is the main factor in the evolution of colonial social structures. If information acquisition is an explanation for the evolution of colonies, it may also form part of an explanation for structures that we previously believed to be understood.

Agent based modelling has been used in many studies of animal behaviour as it enables experiments that attempt to explain the emergence of macro-level patterns from the behaviours of individuals at the micro-level. This approach, therefore, lends itself to modelling the effect of information acquisition pressure on members of a group in order to observe emergent social structure.

We explore how an individual's information acquisition strategy varies depending on the patchiness and ephemerality of resources within its environment. Through studying how their dependence on socially acquired information varies, we are able to draw conclusions regarding the likelihood of aggregation in a given environment.

Chapter 2

Biological Background

This chapter aims to provide an overview of the biology necessary to understand how natural selection acts on the behaviours that individuals exhibit. Situations in which the ability to acquire information is thought to provide an advantage are then examined. Finally we explore the social structures that might arise from these behaviours.

2.1 Natural selection

Gregor Mendel's discovery of genetics through his experimentation with plant hybridisation would seem to be a sensible starting point for a theory of evolution by natural selection. However, Mendel's work lay 'undiscovered' until the early 20th century which makes Darwin's famous theory of evolution by natural selection all the more remarkable.

Natural selection is the theory that naturally arising differences in individuals can give some individuals a better chance of survival than others. If these advantages are passed down to the offspring then they in turn will have a better chance of survival than the offspring of other adults. Over several generations the process of natural selection will result in a greater proportion of the population with the advantageous trait.

Crucial to the understanding of natural selection are the concepts of variation and inheritance, the basis of which is the gene. A gene is a length of deoxyribonucleic acid (DNA) which codes for a polypeptide and in sequence with all of an individual's other genes, make up the genotype. Variation, between individuals, refers to differences in a gene at a particular location (*locus*) in the genetic sequence. These variants of genes are called *alleles*. Different alleles are caused by genetic mutations which can occur by errors in DNA replication or from DNA damage. The majority of mutations that have phenotypic effects[1] are neutral or disadvantageous to the individual. In sexually reproducing species, for a mutation to be heritable it must occur in germ-line cells, the cells that carry genetic material that will be passed on to offspring, such as spermatozoa.

[1]The observable traits of an individual determined by the genotype and environment of the individual.

2.1.1 Inclusive fitness

One of the most often referred to elements of natural selection is the notion of 'survival of the fittest'. Fitness is a measure of the success of an individual in proliferating its genes. In Darwinian natural selection, fitness focused on the reproductive success of the individual.

Hamilton (1964) extended this, in his theory of inclusive fitness, by suggesting that an individual's success should not just be measured by the number of offspring that they have managed to create but also the reproductive success of their relatives. This theory revolves around the concept that it is not only one's offspring that carry one's genes but any related individual. Any related individual, however distant their ancestry, has a probability of carrying at least some of an individual's genes. As such, the concept of *relatedness* is important to understand and has been at the root of most arguments against inclusive fitness theory. A description of relatedness and its implications for altruism are discussed in section 2.2.2.

Recently, arguments claiming to show weaknesses with the theory of inclusive fitness have been made. Through work attempting to explain eusociality[2], Nowak et al. (2010) note several weaknesses of inclusive fitness, such as limitations on the types of interactions allowed. The reception of the paper has, however, been mixed, with many negative responses, most notably from Gardner et al. (2011). Kin selection, a result of inclusive fitness, has been used to explain the evolution of eusocial behaviour, see section 2.2.2.

2.1.2 Adaptation

Adaptation is the process of natural selection working on an organism's genes to allow them to live more successfully in their environment. An example of adaptation used in most textbooks is that of the peppered moth (*Biston betularia*). At the beginning of the Industrial Revolution in England the peppered moth had light coloured wing patterns which camouflaged them when they settled upon tree trunks and branches. The increasing levels of pollution led to trees becoming blackened with soot, rendering the peppered moth's camouflage ineffectual and leading it to die off due to increased predation. However, a particular morph of the moth, *carbonaria*, 'suffered' from melanism which caused it to develop a dark pattern rather than the typical light pattern. This trait proved beneficial to the moth, allowing it to camouflage itself on the soot covered trees. The melanism was caused by a hereditary allele which meant that the offspring of the *carbonaria* morph of the peppered moth were more likely to survive than their light coloured conspecifics.

It is important to note the role of the environment in the adaptivity of an allele. It was not until the trees were darkened by soot that the melanistic allele become adaptive in peppered moths. Occasionally a mutation that is detrimental to an organism can become adaptive within a particular environment. An example of such a situation is that of sickle cell anaemia, which causes deformation of red blood cells rendering them less effective.

[2]A form of colonial society in which individuals give up their reproductive rights, instead aiding the reproduction and nurture of offspring of a single individual.

However, carrying a single sickle-cell causing allele makes the carrier more resistant to malaria. This fitness benefit causes a greater proportion of those living in tropical and sub-tropical regions to be carriers of the allele. In general, a trait is considered adaptive if it increases the inclusive fitness of the individual.

2.2 Altruism

Four forms of social behaviour are of particular interest to social scientists and biologists: altruism, cooperation, selfishness and spite. Of these four, altruism and spite are the hardest to explain using the standard model of Darwinian natural selection. Spite is defined as taking an action against another individual that inflicts some cost on them but at a cost to yourself. Altruism is taking an action that imparts a benefit on another individual at a cost to oneself.

The difficulty with explaining altruism, in a world in which natural selection is the force driving behavioural evolution, is explaining how a behaviour that benefits other individuals at a cost to oneself could be adaptive. There exist a handful of theories that propound explanations for altruisms existence under certain circumstances. Often, the same mechanisms for explaining the existence of altruism can also be used to explain the existence of spite.

An issue that remains contentious is whether there exists a theory that can explain how eusociality could have evolved. Eusociality involves some individuals within a group giving up their reproductive rights altogether; an extreme form of altruism. This is impossible to explain with a standard model of natural selection as an allele that promotes a behaviour that stops the organism reproducing, and therefore the proliferation of that allele, would swiftly die out. In some species non-reproduction can be triggered under specific circumstances. Although this would not cause the particular allele to die out immediately, without the effects of inclusive fitness the allele would eventually die out.

2.2.1 Reciprocity

Reciprocal altruism is a response to the problem that an individual doing something to benefit another individual without personal benefit, and with an implicit or explicit cost to themselves, would not survive long. However, if an individual can expect to benefit at a later point in time from their act of altruism then this behaviour could be adaptive.

Trivers (1971) describes a mechanism by which *cheaters*, those individuals that fail to reciprocate, can be selected against. He states that if altruists punish cheating by withholding further altruistic gestures and the benefits of the altruistic acts outweigh the cost of reciprocation, cheaters will be selected against. Reputation mediated altruism goes one step further than this. It allows individuals to learn about the likelihood of reciprocal behaviour of individuals, i.e. their reputation, from a third party. It is clear that reciprocity can only be beneficial when the cost-benefit ratio is suitably uneven, that is to say the cost to the

altruist must be lower than the benefit to the beneficiary. Further, the cognitive capacity required to intelligently make decisions regarding which individuals to perform altruistic acts to may be beyond the majority of, if not all, non-human species (Stevens et al. 2004).

Generalised reciprocity

Generalised reciprocity is a theory that strives to explain reciprocity amongst species without the cognitive skills for other forms of reciprocity. The strategy is simple, help anyone if helped by someone. Van Doorn & Taborsky (2012) studied whether different levels of connectivity and modularity within a social network have an effect on the ability for generalised reciprocity to take hold in a society. Their findings, and comparisons with empirical data on a number of species, shows that sparsely connected, highly modular societies can not only evolve generalised reciprocity but are protected against invasion of defectors.

2.2.2 Kin selection

Made popular by Hamilton in the 1960's, kin selection is a by-product of inclusive fitness. It relies on the concept of *relatedness*, a quantitative measure of the likelihood that two individuals share a specific gene. Originally, Hamilton's measure of relatedness was based on "Sewall Wright's Coefficient of Relationship" (Hamilton 1963) but was later reformulated to allow for negative relatedness (when two individuals are less related than two randomly selected, average individuals), by using the corresponding regression coefficient (Hamilton 1970). Since inclusive fitness includes the fitness of relatives as well as the individual, the kin selection theory states that altruistic behaviour is adaptive if the correct balance between relatedness and cost-benefit is achieved. Hamilton's rule describes this mathematically:

$$rB > C \tag{2.1}$$

where

r = genetic relatedness of the performer to the recipient at the locus for the social behaviour.
B = benefit to the recipient
C = cost the the performer

For kin selection to be effective the altruist must either be able to recognise the relatedness of other individuals or the population must be sufficiently *viscous*. In this context viscosity refers to the flow of individuals in and through populations i.e a more viscous population is one in which individuals do not move far from their place of birth. This increases the chances of interacting with kin without requiring the cognitive skill to recognise relatedness. It has been shown that kin selection can be adaptive in viscous populations without the requirement of relatedness recognition (Čače & Bryson 2007).

It is important to note that relatedness is not, as is commonly misconstrued, equal to the *proportion* of genes that two individuals have in common. Rather, it is the likelihood that two individuals share a specific allele. Kin selection works on the probability of sharing an allele that promotes altruism, "all the remaining genes ... are completely irrelevant to the discussion" (Park 2007).

Many eusocial species are haplodiploidy, meaning males develop from unfertilised eggs whereas females develop from fertilised eggs. This results in sisters being more related to each other (3/4) than to their own daughters (1/2). In this situation, females can increase their inclusive fitness to a greater extent by helping their mother to produce more offspring than by producing their own offspring. This, however, cannot be a full explanation of the evolution of eusociality since there exist eusocial societies in which the species are not haplodiploidy as well as non-eusocial haplodiploidy species.

2.3 Information acquisition

In order to discuss how information can be acquired it is prudent to first consider what is meant by information in this context. The standard concept of information is "anything that reduces uncertainty" (Danchin et al. 2004). Dall et al. (2005) extend this with the claim that ambiguity reduction is not sufficient, when concerned with behavioural and evolutionary ecology rather than molecular or neuro-biology, and that for it "to be informative, it must be 'useful' to animals".

Information can be split into two forms, classified by the method of acquisition: *personal information* and *socially acquired information*[3]. Personal information is acquired by an individual through their interactions with the environment. Euclidean maps used by many species of primate, including chimpanzees (Normand & Boesch 2009, Normand et al. 2009), gibbons (Asensio et al. 2011), spider monkeys (Valero & Byrne 2007) and white-faced saki monkeys (Cunningham & Janson 2007) are examples of personal information regarding resource locations. However, personal information is not limited to food patch locations. Predation risk at different locations and the distribution of conspecifics of the opposite sex are both important in informing the behaviour of individuals.

2.3.1 Socially acquired information

Socially acquired information is gained through observation of conspecifics, and in some cases heterospecifics (Goodale et al. 2010). It can be subdivided further into *signals*, purposeful communication of information, and what Dall et al. (2005) refer to as 'inadvertent social information'.

[3]The classifications of information used here, detailed in figure 2.1 , were laid out by Dall et al. (2005), which in turn was based on work by Danchin et al. (2004).

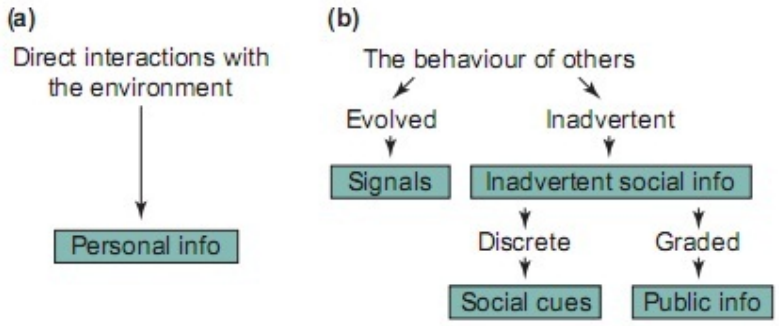


Figure 2.1: The classification of potential sources of information available to an animal according to whether information is obtained via direct interactions with its environment [personal information (a)] or from observing the behaviour of others [socially acquired information (b)]. Personal information can be deliberately (evolved signals) or inadvertently provided. If other animals inadvertently produce the socially acquired information, it can be further differentiated according to whether it provides discrete (social cues: e.g. presence or absence of a predator) or graded information (public information: e.g. amount of food available in a patch) to the information gatherer. (Dall et al. 2005)

Inadvertent social information

Social cues *Social cues* form the first part of the inadvertent social information class proposed by Dall et al. (2005). This refers to discrete information about the immediate surroundings of another individual. *Gyps* vultures dropping their legs while gliding indicates to others that they have spotted a carcass to feed on (Dermody et al. 2011). These cues are what animals taking advantage of local enhancement rely on, see section 2.5.2. This can create an *information cascade* as the cue causes others to adapt their behaviour and, in doing so, cue further individuals (Dall et al. 2005). The result can be vultures from up to thirty five kilometres away being informed of the location of the carcass. However, cueing is not limited to food locations. An animal fleeing is a cue to others of potential impending danger which can also cause an information cascade, as is commonly seen in pigeons (*Columbia livia*). Giraldeau et al. (2002) argue that, due to the limited detail of information transferred by a social cue, information cascades can lead to sub-optimal behaviour.

Public information The second part of inadvertent social information is *public information*. This information refers to the quality of a resource in a 'graded' rather than discrete fashion. A study of an osprey colony showed that the birds were able to deduce the quality of a potential food patch from the type of fish with which a conspecific returned to the colony (Greene 1987). If an individual returned from foraging with a type of fish that was known to school, this would be regarded as good quality information and a large number of birds would depart in the direction that the returning osprey came from. If, on

the other hand, an individual returned with a fish that was known to live solitarily or in smaller groups, birds were much less likely to use this information. Danchin et al. (2004) give many examples of public information acquisition and use in foraging, habitat copying, mate-choice copying and damage limitation and danger aversion.

The benefit of being able to socially acquire information is that there is a greatly reduced cost in acquiring the information. The individual no longer has to search their entire habitat in order to learn about it. However, for individuals that excel at acquiring personal information, their advantage is nullified if they are unable to prevent others from 'stealing' their information. Indeed there will be a cost to the more skilled individual from increased competition at resource locations that are shared. As is stated in section 2.5.1, it is believed that in social structures that increase the probability of inadvertent social information acquisition, all individuals should have an equal chance of finding resources during a search. If searching ability becomes too unequal, the costs, to the more able, of sharing information would begin to outweigh potential benefits of group living. Thus, if there is a large skill gap in foraging ability, it is better for the more skilled individual to live solitarily rather than in a group. However, there may well be other benefits to living in a group that outweigh the costs of parasitism to the individual, see section 2.5.

Signals — Information donation

The other branch of socially acquired information is information that is transferred purposefully. The signals that species use to transfer information are incredibly varied: from the waggle dance of honey bees (*Apis spp*) (Riley et al. 2005) to the pheromone trails of ants (*Formicidae*) (Sumpter & Beekman 2003) and from the warning colouration, *aposematism*, of poison dart frogs (*Dendrobatidae*) (Darst et al. 2006) to the chest-beating of eastern gorilla (*Gorilla beringei*). It is possible to split these signals into two classes; the communication of information about the signaller, and the communication of information about the signaller's environment.

Darwin believed a behaviour that benefited another individual by giving them information about the environment could not be selective[4]. This lead him to theorise that the purpose of communication was to inform others, accurately, of one's internal state. An oft used example when considering communication is that of the male peacock. In order to attract a mate the male peacock's tail is highly decorative. This decorative tail is used by the peacock to inform potential mates of its suitability; the more lustrous the plumage, the more desirable the peacock.

However, suppose that a genetic mutation allowed a peacock to lie about his suitability as a mate by making his tail more elaborate than would normally be representative. Thus, the liar gains an advantage over the honest signaller, the lie proliferates and the honest

[4] A few situations in which communicating environmental information can be beneficial, without requiring inclusive fitness theory, have been noted. For example, Trivers (1971) states that alarm calls, usually thought only to benefit neighbours, can have a benefit to the individual by not allowing a predator to get used to predating the caller's species.

signallers die out. Over time females would learn to ignore the 'information' given by the males' tails altogether.

The handicap principle If, however, there is a fitness handicap to the signaller, such that only a fit individual can produce the signal, then dishonesty cannot be adaptive (Zahavi 1975). Continuing with our analogy of the peacock, the costs to the peacock of a more extravagant tail should be considered. The energy required to grow and maintain an extravagant tail could be better used in foraging, mating and predator evasion. Further, the more splendid the tail, the more obvious a target for predation the peacock becomes. If these costs are taken into consideration, only the fittest males could maintain such a tail and survive. If a peacock mutated to exaggerate their plumage, they would not be able to incur the costs of supporting the tail and would die out.

Smith (1994) showed, using the Philip Sydney game, that it is possible for signals regarding one's internal state to be reliable and free if the preferences, of the signaller and receiver, for the order of possible outcomes are the same.

Communication as manipulation Communication as a tool for manipulation rather than information transfer was proposed by Dawkins & Krebs (1978). Exaggerated sexual swellings are used by some primates to advertise sexual receptivity. It would seem to be unnecessary for a female to incur even the small cost involved in this form of signalling if the purpose of the signal is truly to advertise the optimal time for fertilisation. However, it seems that this form of communication has evolved to be used for the manipulation of males for protection and paternity confusion (Nunn 1999).

2.4 Decision making

Decision making has been the topic of much research in economics and psychology (Edwards 1954). When presented with more than one option, an individual must decide which one will provide the greatest benefit while requiring the least cost[5]. Simon (1972) proposed that one should consider two types of decision maker: *maximizers* that try to arrive at the optimal decision and *satisficers* that settle on a *satisfactory* option. Determining the optimal decision requires an exhaustive search which is computationally expensive. As such, it is likely that all decision making undertaken in nature is a search for a satisfactory, rather than optimal, option.

The usefulness of information to an individual is to inform the decision making process. Whether it be information regarding which females are in oestrus guiding mating decisions or information about the location of resources directing foraging paths, the informed individual has an advantage over uninformed conspecifics. However, the greater the amount

[5]This is not actually always true. Behaviours such as spite occur even though there is no evident benefit to the actor.

of information held by an individual, the greater the task of making a decision based on this information. This leads to a strong correlation between working memory capacity and reasoning ability (Kyllonen & Christal 1990).

When modelling movement decisions in simple organisms random walk models have been very successful and have dominated the literature (Boyer & Walsh 2010). However, many examples exist of animals using information to inform decisions. Some species, such as gibbons (Asensio et al. 2011) and spider monkeys (Valero & Byrne 2007) exhibit the ability to use Euclidean maps to plan routes when foraging. In an extreme example of route planning, white-faced saki monkeys (*Pithecia pithecia*) plan their routes so rigidly that they will not stop at fruit trees that they pass en-route to their destination (Cunningham & Janson 2007).

2.4.1 Group decision making

Decisions become more complicated when an individual is part of a group. Their own personal information is no longer the only information that can inform their decisions; the behaviours of others may also have a say. It used to be commonly believed that group movement was initiated by a leader that had a high social status. However, it is now known that this responsibility can be spread over many individuals that do not hold dominant positions (Petit & Bon 2010). Behaviours which seem to show dominant individuals leading can often be explained by observations of pre-departure behaviours. Silverback mountain gorillas appear to initiate group movement by quickly moving in a particular direction but if vocalisations of other individuals are taken into account, it appears that it is group consensus that causes the group to move (King & Sueur 2011).

In communities in which group cohesion is important, voting can take place as to which direction to move in. Tonkean macaques (*Macaca tonkeana*) vote by moving away from the group in their proposed direction (King & Sueur 2011). Most of the time only one direction is proposed but if more than one is suggested, they wait until a threshold of individuals in each direction has been reached. They then choose the direction in which the majority of individuals have moved. Voting behaviour is also exhibited in African buffalo (*Syncerus cafer*) (Prins 1995) and Hamadryas baboons (*Papio hamadryas*) (Kummer, 1968 as cited in (King & Sueur 2011)).

A study by Kerth et al. (2006) concluded that Bechstein's bats tend to follow the majority roosting decision except when they have personal information that conflicts with said decision. In these cases the fission-fusion social structure of the bats allows the individual to follow their own information. Such studies suggest that there is a hierarchy of information: negative personal >socially acquired >positive personal. It should be noted that an individual cannot infer positivity or negativity of socially acquired information when it comes to group movement. If a group sets off in one direction, it does not mean that all other directions would have negative consequences if moved towards. However, this hierarchy may depend on the environment that the individuals inhabit, which effects the reliability of personal information, and the individuals ability to accurately gather social information,

effecting the reliability of socially acquired information.

2.5 Colonial societies

There are several structures of society that are exhibited in the animal kingdom; from the solitary nature of most *felidae* to the highly structured eusocial systems of *termitoidae*. Social structures can be broken down along two lines: the level of aggregation and the level of hierarchy.

As with all animal social behaviours, understanding the costs and benefits of aggregation are important if one wishes to understand how the social structures evolved. The most obvious cost of group living is the increased competition that arises from having more conspecifics attempting to utilise the same resources. Further costs include increased likelihood of detection by predators and increased chance of transmitting parasites and pathogens (Silk 2007). The benefits include increased predator detection and repulsion, potentially reduced thermo-regulation costs (Hayes 2000) and increased information acquisition opportunities (Garber et al. 2009).

One such form of society is the colony, in which individuals aggregate at a single location for breeding and/or roosting. Many species, but particularly birds and insects, exhibit colonial behaviour and much research has been undertaken into the mechanisms for such tightly packed structures to have evolved.

2.5.1 Information centres

One hypothesis that aims to explain aggregation into colonies is the information centre hypothesis (ICH). It suggests that the main pressures on individuals to aggregate is the need to gather information, particularly concerning food patches in sparsely resourced ecosystems (Ward & Zahavi 1973). Colonies act as hubs for the sharing of information, improving individuals' chances of feeding by reducing the cost of searching for food by taking advantage of group search.

Richner & Heeb (1995) state eight assumptions that are often made when investigating the information centre hypothesis and that, without the presence of these eight conditions, negative results should not be used as evidence against the hypothesis. They are:

1. Food patches are sparsely distributed in space and/or ephemeral in time.
2. Food patches are abundant enough to, at least partially, negate increased competition.
3. The lifetime of a food patch is such that a return trip is worth-while.
4. Foragers return to the colony after a successful trip.
5. It is possible to distinguish between successful and unsuccessful foragers.

6. Successful foragers return to previous feeding sites.
7. Success in foraging is due to chance rather than ability.
8. There is a greater chance of success if an unsuccessful forager follows more successful foragers than if they do not.

Barta & Giraldeau (2001) make an important, and often overlooked, point that a distinction needs to be made between breeding colonies and communal roosts. The costs to a successful forager of returning to a communal roost could be negated by not returning, saving travel time and information parasitism. In such situations the advantage is given to the successful forager that remains solitary (Richner & Heeb 1995). Therefore, information exchange fails to explain the evolution of aggregation into colonies and reasons such as predation avoidance seem more acceptable. This is not to say that information exchange does not occur at the roost, just that it is not the driver for aggregation.

However, once an individual has decided on a breeding location, they have no choice other than to return in order to feed their offspring. Other conspecifics may choose to nest at the same location because of the information that will be available to them at the nesting site. As such, the unavoidable parasitism of information at breeding colonies may be a sound explanation for the evolution of colonies.

If birds roost suitably close to relatives within the colony, then incurring the cost of returning to the roost, as a successful forager, may be negated by the inclusive fitness gains from sharing information. Richner & Heeb (1995) states this as the likely reason why "hymenopteran colonies function as a centre of information exchange about the location of distant food patches". As such, eusocial colonies seem to be the one easily justified example where information exchange may have been the driving force for aggregation.

Zahavi (1996) makes an interesting argument regarding a mechanism to dissuade individuals that are weaker, and therefore less likely to contribute information, from joining a group. He proposes that the pre-roost display maneuvers, undertaken by large numbers of conspecifics, act as a method of measuring ones capabilities against others in the flock. If an individual decides to join a feeding group in which the members of the group are more capable than them, then, as the weakest member, that individual is the most likely group member to be predated. In this situation the interests of the flock and the predator are aligned. Thus, the costs associated with sharing information can be alleviated without the need for mechanisms that ensure reciprocation.

The point should be made that information transfer at aggregation sites does not have to be one-way. Norway rats (*Rattus norvegicus*) exchange information regarding the edibility of food by smelling the breath of other rats (Galef 1991). Both rats in this situation gain information about edible foods if both rats have recently eaten.

A number of empirical studies have be undertaken attempting to prove ICH (Richner & Heeb 1995). One such study by Wright et al. (2003) shows that 'knowledgeable' ravens (*Corvus corax*) initiated departures from the roost and carried out pre-roost acrobatic

display flights as a signal to conspecifics. A field study of ospreys observed the birds utilising public information acquired at the nesting site (Greene 1987). Interestingly, ospreys exhibit a wide range of social and foraging behaviours, nesting solitarily as well as in colonies. This lends itself to the interpretation that ospreys are able to vary their social structure to best fit the environment which they inhabit. Changing social structure depending on external factors does not even require any great cognitive capacity. The gregariousness of desert locusts (*Schistocerca gregaria*), and in turn their desire to remain part of a group, can be changed through a variety of mechanisms such as 'tactile stimulation' which, in nature, happens more consistently when they are surrounded by conspecifics (Simpson et al. 1999).

2.5.2 Local enhancement

Several arguments against the information centre hypothesis have centred on the fact that behaviour resembling that predicted by the ICH can be explained by other processes, such as *local enhancement* (Mock et al. 1988) and the *recruitment centre hypothesis* (RCH) (Richner & Heeb 1995).

Local enhancement and ICH may well appear similar so an important distinction needs to be made between the two. Richner & Heeb (1995) state that the difference

> concerns the location of information transfer between individuals: local enhancement occurs at the food patch and the increase of group size arises as a consequence of birds cuing on already foraging animals. An information centre is localized away from the food patch and supposedly arises as a consequence of animals seeking information from successful foragers about the location of the distant food source.

Models have been developed that support the idea that colonies could have evolved due to the benefits of local enhancement (Buckley 1997, Dermody et al. 2011). Barta & Giraldeau (2001) point out that this does not rule out ICH as a factor in colony evolution.

2.5.3 Recruitment centre hypothesis

The recruitment centre hypothesis depends on the assumption that resources are better exploited as a group rather than as an individual. Recruiting others to a feeding location can also be beneficial in reducing predation risk by the dilution effect (Richner & Heeb 1995). It is argued that colonies evolved primarily to allow easy access to groups of individuals for recruitment for feeding trips [6]. The need to recruit a group could be due to the need to force another group from a resource location or the requirement of a larger number of individuals to be able to access a food source, such as hunting large prey. In this way,

[6] I use the term 'feeding trip' here to mean a trip to a known feeding location rather than a trip to search for food.

a colony may act as a "recruitment centre for successful foragers and as an information centre for the unsuccessful ones" (Richner & Heeb 1995).

The primary problem with the RCH is one that also occurs with the ICH; why go searching for resources if others will do it for you? By modelling both ICH and RCH as a producer-scrounger game, Barta & Giraldeau (2001) shows that an equilibrium will be reached between individuals that search and those that wait. The advantage for the searchers is the extra food that they gain by being first to find the patch.

Chapter 3

Modelling Background

A model is a simplified representation of a system, usually with unnecessary or irrelevant parts omitted. This allows the testing of hypotheses through the removal of parameters that are thought to be extraneous. Though the results of experiments using models can help to justify a hypothesis, it should be held in mind that experimentation on a model can only ever *prove* something about the model. Empirical evidence of experimentation on the system being modelled is required for comparison in order to evaluate the validity of the model. Modelling is a tool that can be used when empirical experimentation is costly.

Lenski's evolution experiment with *E coli* has been running since 1988 and has only recently reached 50,000 generations (Lenski 2012). Far slower has been Garland's selective breeding experiment in house mice (Garland et al. 2011). Since 1993 it has managed only 50 generations. In the study of evolutionary biology, simulations allow experimenters to observe evolution over thousands of generations in a tractable time frame, though with a more restricted genomic and phenotypic plasticity.

3.1 Modelling approaches

Several forms of modelling and experimentation exist in evolutionary and social biology. Agent based modelling is considered in detail and a review of two alternatives is undertaken below.

3.1.1 Agent Based Modelling

Agent based modelling (ABM) aims to discover macro-level outcomes emerging from micro-level behaviours and interactions of co-located agents. It does this by specifying rules that agents adhere to and allowing the agents to interact, with each other and their environment, according to those rules. The link between the micro and the macro is still a contentious issue with some claiming that actions only occur at the micro level and macro level obser-

vations only emerge from these actions (Squazzoni 2008). Others argue that the existence of a macro-level social structure has an influence on the individuals. Therefore, it acts as well.

ABM has been used in a variety of fields such as battlefield simulation (Berryman 2008), industrial supply network modelling (Van Dyke Parunak et al. 1998), intelligent building monitoring (Davidsson 2001) and of course socio-ecology (Evers et al. 2012, Sellers et al. 2007, Bryson et al. 2007). Since its inception it has been used for simulations of animal behaviour and has become an increasingly useful tool for sociologists and biologists alike. A "model of group decision making in baboons" (Sellers et al. 2007) demonstrated how a model can be validated by checking its predictions against field observations. It also showed that failures in the model can highlight "key elements that [are] missing from the field data". Bryson et al. (2007) justify the use of ABMs for scientific experimentation and demonstrate that they can stand up to augmentation when part of the model is disputed.

Action selection Action selection is described by Bryson (2003) as "the means by which an autonomous agent solves the ongoing problem of choosing what to do next". Four models of action selection, of increasing complexity, are outlined in the paper, with the suggestion that the least complex model possible should be used. The two basic levels of action selection are 'environmental determinism' and 'finite state machines'. The more complex 'basic reactive plans' and 'POSH' introduce frameworks for opportunism and the ability to juggle multiple goals respectively.

ABM platforms

There exist several platforms for the development of simulations of agent based models. A number of reviews of ABM platforms have been undertaken and the analyses of two of them will be discussed here. Functionality and execution speed are primary concerns but, due to limited project time, ease-of-use and quality of documentation are important as well. Nikolai & Madey (2009) recently reviewed available ABM platforms including their system requirements, programming language and primary field of use, though did not make a comparative analysis of any of the systems.

- NetLogo: Ease-of-use seems to have been a central consideration when NetLogo was initially designed. It is the most well supported platform in terms of documentation and has an active community developing additional functionality. It lacks certain useful features such as scheduling actions to occur in the future (Railsback et al. 2006). For fast prototyping or for development of models without a great deal of computational complexity, NetLogo is a good choice. Berryman (2008) claims it "is a good environment for exploring structure formation".
- Swarm: Available in both Objective-C and Java flavours, Swarm provides a "toolbox for ABMs" (Railsback et al. 2006). Execution speed experiments show that Swarm

is surprisingly slow for all but the most simple models (Railsback et al. 2006). The Java version seems to have too many drawbacks to be considered as a good platform, especially with the other Java based platforms mentioned. Objective-C Swarm is the oldest of the ABM platforms which makes the lack of documentation surprising.

- RePast: Developed as a Java alternative to Swarm with the clear goal of supporting social scientists. Railsback et al. (2006) conclude that RePast is "the most complete Java platform" but has a handful of complaints regarding design decisions. Again, documentation and accesibility for beginners are weaknesses.
- MASON: It was designed to be faster than RePast for computationally demanding simulations but generally only acheives this by a small margin (Railsback et al. 2006). The fastest option for complex models but a lack of documentation and useful tools mean that development would be a long process. Berryman (2008) claims that it "should be used where speed and/or sophisticated batch runs are required" and that it is "an excellent choice for exploring adaptation".

3.1.2 Alternative approaches

Evolutionary Game Theory

Evolutionary game theory is a form of game theory developed by Maynard Smith to attempt to explain ritualised conflict. It works by comparing the relative superiority of one strategy over another in a particular situation (*game*). There is no spatial concept in a game theoretic model and the temporal aspects of a system are modelled only through iterations over the game. This restriction removes context from behaviours thus making the model less "natural" (Hemelrijk 2004).

Equation Based Modelling

As in agent based modelling, equation based modelling (EBM) views the world as encapsulated by two entities: individuals and observables (Van Dyke Parunak et al. 1998). Individuals are active in their environment and separate from each other. Observables are measurable characteristics of the system, or individuals within the system. Van Dyke Parunak et al. (1998) gives the example of individuals as particles within a box. Observables could be the velocity of an individual particle or the pressure in the box caused by the collection of particles.

EBM works by defining a set of equations that encapsulate relationships between the observables. The actions of the individuals do not play a part in the equations. It fundamentally differs from the ABM approach because it tries to "express relationships among observables" with no regard for the behaviour of individuals (Van Dyke Parunak et al. 1998). Van Dyke Parunak et al. (1998) conclude that ABM's are "better suited to domains where the natural unit of decomposition is the individual rather than the observable or the

equation" which is usually the case in biology due to the ease of drawing analogy between agent and organism.

Part II

Experimentation

Chapter 4

Introduction

We aim to explore how variations in the environment in which an individual lives affects that individual's information acquisition strategy. Information regarding resources can be gathered through one's own exploration of the environment or from observation of the actions of conspecifics. Both of these forms of information acquisition have costs associated with them, whether it be energy expenditure from searching for food or increased competition at food patches if acquiring information socially. As such, the best information acquisition strategy that an individual can use will depend on how the resources 'behave' within the environment.

An exploration into how the patchiness and ephemerality of resources within the environment affects the information acquisition strategies used by individuals is undertaken. An agent-based model is used to show trends in information acquisition strategy in a population of colonial agents. The agents are able to acquire personal information through *searching* the environment for resources. Alternatively, they can acquire information socially by following other agents on their foraging expeditions. Each agent has a level of preference for using one strategy over the other. This preference is passed on to their offspring, with a degree of variation, which leads to a fitness differential between conspecifics, if there exists a benefit to favouring one strategy over the other.

The results of our experiments into the effects of resource patchiness agree with our hypothesis, that the patchier, the environment the greater the benefit of acquiring information socially. Further, our model exposes the effects on population level of occasionally receiving only a partial benefit from a resource location. Our exploration of the effects of resource ephemerality show a similar pattern, that the shorter the lifetime of resources the more beneficial the use of a social information acquisition strategy. However, a curious continuation of the trend, when resources are so short lived that they cannot be returned to, exposed a flaw in the method of locating resources.

Then, we look at some of the changes we made to our model throughout the experimental process. Finally, we discuss possible ways to extend the model and areas into which future work might venture.

Chapter 5

The Model

In order to explore how the environment might impact the way in which colonial animals acquire information, we used agent-based modelling to create a model in which we can vary the properties of resources within an environment. We are able to use this model to measure how the strategy for the acquisition of information by agents adapts over a number of generations.

5.1 Environment

The environment in which the agents act is a wrap-around plane, in which the bottom edge is a continuation of the top edge and likewise for the side edges. The dimensions of the plane, 400×400, are large enough that an agent cannot take advantage of the toroidal nature of the surface as it is larger than their foraging range. The plane needs to be continuous to avoid peculiar edge-effects. Further the plane needs to be large because, for animals that roost at a single location, it is costly to move far away from the roost as any distance that they travel away they have to cover on the return journey, doubling the cost of the trip.[1] It is clear that an animal should not be able to, for example, travel ten miles in a straight line away from a location and return to that location with only a five mile trip, as can happen on a toroidal surface.

Within the environment there are three types of object: the agents that inhabit the environment, the resources on which the agents 'feed' and the roost to which the agents return after foraging. The roost is a 1×1 square located in the centre of the environment. When multiple agents are resting at the roost, they are at an identical location to each other. As such, they can observe the behaviour of all other agents in the roost. This is satisfactory for this experiment, however, only being able to observe conspecifics in your

[1] We use the term roost here to mean the home location for all members of the colony. We do not make the traditional distinction between a roosting colony and a breeding colony. The difference between the two is important when considering the motivation for a successful forager to return to the roost/nest but is not modelled here.

Table 5.1: The properties of a resource.

Property	Description
magnitude	Amount of 'food' remaining. If the magnitude reaches 0 the resource 'dies'. All resources in an experiment are 'born' with the same magnitude equal to *total-resource/num-resource-locations*.
lifetime	The number of ticks remaining until the resource expires.

immediate surroundings within a roost, rather than all individuals in a roost, may be important in protecting the group from infiltration from individuals that are able to withhold information, see section 5.4.2.

5.1.1 Resources

Resources in the environment represent feeding locations. Each resource has two properties in addition to it's spatial position: *magnitude* and *lifetime*, as described in table 5.1.

When each experiment is set up, a number of resources equal to *num-resource-locations* are spawned into the environment.The resources are located randomly at a distance of 100 units from the roost, effectively forming a ring around it. When a resource expires, from food exhaustion or lifetime expiration, a new resource is spawned. This allows us to vary the number of resource locations while maintaining a constant level of food within the environment and a constant cost to the agent of retrieving known food.

The probability of an agent finding a resource is varied through the number of resources in the environment. The reliability of resource information can be changed by varying the lifetime of the resources. Information reliability also changes by varying the number of resources, as this affects the amount of food held by a resource and, in turn, the rate at which the resource will be exhausted.

5.2 Agents

Agents within the environment eat, breed and die. The life of each agent revolves around a basic forage and return behaviour, in which agents leave the roost in order to find and eat food and then return to the roost. This forage and return behaviour mimics that seen in several colonial species (Greene 1987, Horn 1968). The agents in our model follow a rule set that forces them to return to the roost after foraging. However, the motivation for a successful forager to return to the roost is at the heart of most arguments against the information centre hypothesis (Richner & Heeb 1995). Possible solutions to this problem were discussed in section 2.5 but our initial model does not explore these mechanisms.

Table 5.2: The properties of an agent.

Variability	Property	Description
Variable	energy	The current energy level of the agent. Replenished through 'feeding' at resource locations. It is decremented by 1 each tick by virtue of the agent being alive. If the agent is active outside of the roost then it is further decremented by a value equal to *forage-cost* each tick.
	age	The number of ticks the agent has been alive for. The agent dies if its age reaches the value of *max-agent-lifespan*.
	state	The current state of the agent. See figure 5.1.
	last-birth	The number of ticks since the agent last 'gave birth'. If the agent has not produced offspring in a number of ticks equal to *birth-interval* they will give birth when next at rest in the roost. See section 5.2.1.
	known-resources	A list of the resources that the agent knows about. This represents the personal information possessed by the agent.
	targeted-resource	A resource that the agent has decided to feed at.
	following-who	Another individual that the agent has decided to follow. This represents an attempt to socially acquire information.
	rest-time	The number of ticks that the agent has been at rest in the roost.
	forage-time	The number of ticks that the agent has been active outside of the roost while searching, feeding or following. If this reaches *max-forage-time* the agent will begin to return to the roost.
Fixed at birth	info-weighting	The value that the agent uses to decide whether to socially acquire or personally acquire information when making a foraging decision. See section 5.2.1.
	info-weighting-param	The value that is used to calculate the agent's *info-weighting*. The *info-weighting-param* of an agent's offspring varies 'slightly' from that of the parent.
Constant	vis-distance	The radius within which an agent can see.
	move-distance	The distance an agent can move in a single tick.

5.2.1 Behaviour

The actions that an agent carries out each turn are dictated by their current state, as shown in figure 5.1. Each agent is born at the roost in the *resting* state. The basic algorithm carried out by each agent is described in algorithm 1.

Algorithm 1 The agent's sequence of actions for each tick that it is alive

```
while alive do
    decrement energy
    increment age
    increment last-birth
    if energy ≤ 0 or age > max-agent-lifetime then
        die
    else
        if any resources in vis-distance then
            update known-resources
            target closest resource
        end if
        decide whether to transition to another state
        take relevant action
    end if
end while
```

The "relevant action" is determined by the current state of the agent. The actions undertaken in each state are described below.

Resting

While an agent is in the roost, they are at rest. During each tick an agent spends at rest, they attempt to make a decision regarding *how* to go foraging. If an agent has knowledge of the location of one or more resources, they will select one of their *known-resources* at random to be their *targeted-resource* and transition into the *feeding* state, see section 5.4.4. An agent is not aware of the exhaustion of a resource until they have moved to within their visible range of the location. This means that the agent's list of *known-resources* may be, and in some situations is likely to be, populated with erroneous information, see section 5.4.3.

However, if the agent does not have any information regarding resource locations they make a decision regarding how to acquire such information. Based on their *info-weighting* they choose whether to attempt to gather information personally or socially; the lower their *info-weighting*, the more likely they are to try to socially acquire information. If their current energy level is above *max-energy-level*, they do not make a decision about leaving until their energy level falls below the threshold, see section 5.4.7.

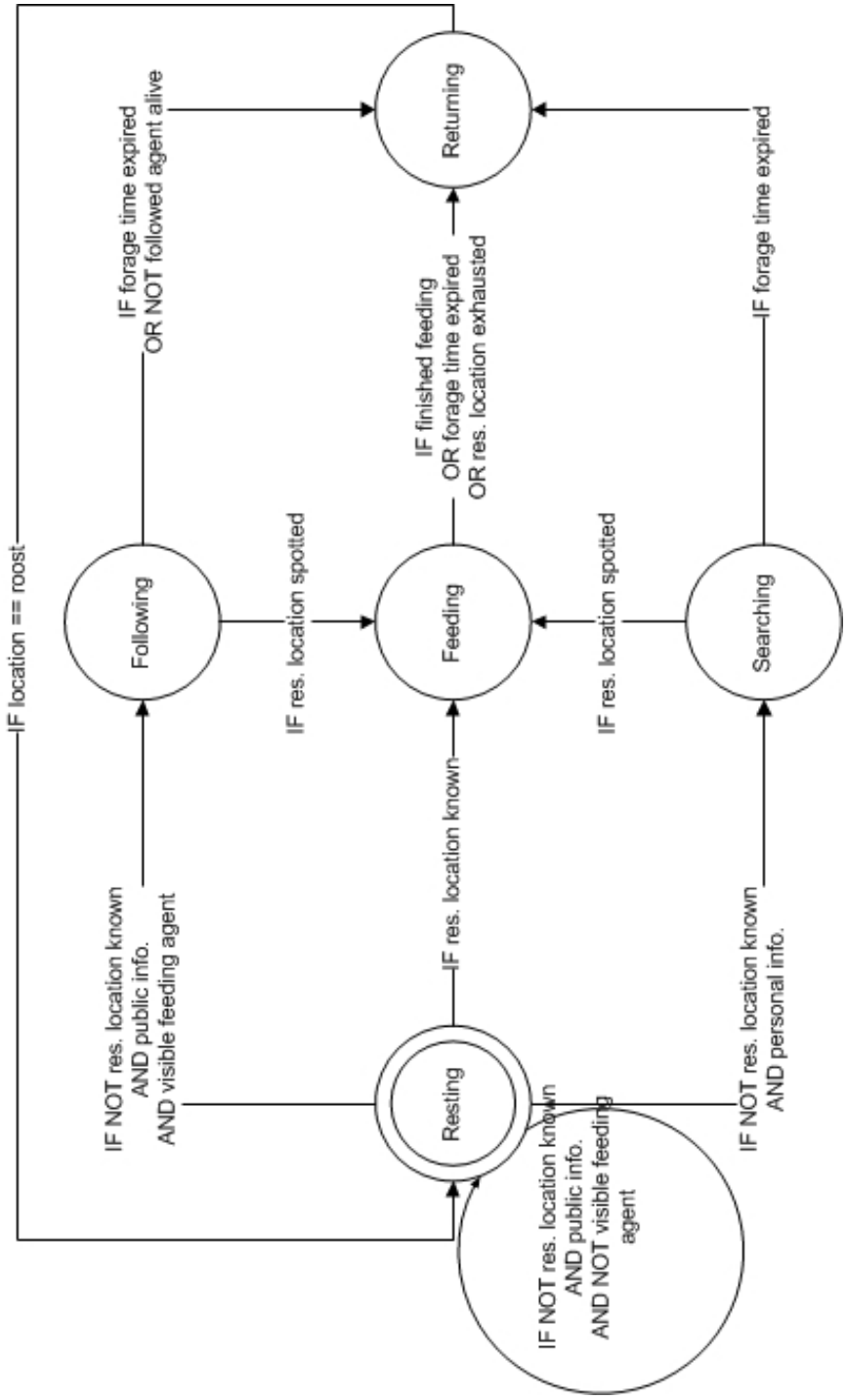


Figure 5.1: A state machine describing the behaviour of an agent. The agent can die in any state if their *energy* is 0 or less or if their *age* is greater than the *max-agent-lifespan* set at the beginning of the experiment.

If a personal approach is decided upon, the agent will transition into the *searching* state. If, on the other hand, the agent chooses to socially acquire information, they look at all the other agents currently visible to them and observe which ones are leaving the roost in the *feeding* state, see section 5.4.2. If there are one or more agents in the set of observed feeding agents, one of them is selected at random to be followed, see section 5.4.4. If there are no observable feeding agents, the agent remains at rest in the roost. The agent can only remain in the roost for a number of ticks equal to *max-rest-time* before they are 'forced' to leave, see section 5.4.6. This is done by making them go searching.

Breeding Breeding is undertaken while at rest in the roost. An agent breeds asexually, giving birth to offspring at a maximum rate of one every *birth-interval* number of ticks. Agents are only able to produce offspring if their current energy level is greater than *max-agent-energy* $\times$ *birth-energy-ratio*. At birth, the offspring is born with an *info-weighting-param* that is varied by a random value, selected from a normal distribution with $\mu = 0$ and $\sigma = 0.05$, from that of their parent's. This is the mechanism of variation in the population that gives rise to a fitness differential dependant on the resource patchiness. The *info-weighting-param* is used to calculate the *info-weighting* of an agent using a sigmoid, logistic function:

$$info\text{-}weighting(\alpha) = \frac{1}{1 + e^{-\alpha}} \qquad \text{where } \alpha = info\text{-}weighting\text{-}param$$

The advantage of using a sigmoid function is that it is a continuous function with a defined maxima and minima. Through preliminary experimentation we saw that this allows the varied trait, *info-weighting-param*, to continue to trend beyond the point at which it may seem redundant, as the *info-weighting* may already be at its limit. This continued adaptation allows agents to protect against the possibility of their 'grandchildren', and further generations, slipping back to a less advantageous form of the trait.

Feeding

An agent enters the feeding state when they have decided on a *targeted-resource* to feed at. They can target a resource either by seeing one while out foraging or by selecting one from their *known-resources* when at the roost. During each tick, they move in a straight line towards the chosen resource. When the agent arrives at the resource they 'eat' some of it, replenishing their *energy* by an amount equal to *food-benefit*, decrementing the resource's *magnitude* by the same amount. After the agent has fed, or if they see that their *targeted-resource* has been exhausted, the agent begins to return to the roost. If, while moving towards their *targeted-resource* they come across another resource, the agent will change target and feed at the visible one. If there are many visible resources the agent will select the closest resource to feed at.

Searching

When an agent decides to leave the roost *searching* for resources, they undertake a random search. When they initially leave the roost, they rotate to a random heading and move in that direction a distance equal to *move-distance*. For the ticks in which they are searching after they have left the roost, they rotate their direction of movement by a random number of degrees, selected from a normal distribution with $\mu = 0$ and $\sigma = 30$, from their previous heading and move a distance equal to *move-distance* in that direction. If any resources become visible they will target one of them. If they do not manage to find a resource within a number of ticks equal to *max-forage-time* they will begin *returning*.

Following

On leaving the roost, if the agent has decided to follow another agent, they orient themselves to face the followed agent's current position and move a distance equal to *move-distance* in that direction. If, while following another agent, a resource is spotted, the agent enters the *feeding* state and goes to feed at that resource rather than continuing to follow the agent. It is likely that the followed agent would also have spotted the resource and moved to feed at it as well. If they followed agent dies before a roost location is spotted, the follower begins to return to the roost.

Returning

If an agent has finished feeding or the amount of time they have spent foraging has exceeded *max-forage-time*, they begin to return to the roost. The agent sets its orientation directly towards the roost and moves a distance equal to *move-distance* during each tick. When the agent arrives at the roost it enters the *resting* state.

5.3 Experimental Variables

There are a number of variables for setting the initial state of the environment and for the various constants that dictate the behaviours of the agents and resources, outlined in table 5.3. The values used in our experiments for each variable can be found in appendix A.

5.4 Simplifying assumptions

As with any model, we must make some simplifying assumptions about the world we are modelling. Some of these simplifications will be necessary in order to remove them as variables that could interfere with what we aim to measure. Other simplifications are made because we do not feel they are relevant to our experiments.

Table 5.3: The variables used to define the environment, the abilities of the agents and the initial settings for experiments

Scope	Variable	Description
Resource constants	total-resource	The total amount of food in the environment. This is used to calculate the *magnitude*, at birth, of a resource: *magnitude* = *total-resource/num-resource-locations*
	num-resource-locations	The number of resource locations within the environment.
	max-resource-lifetime	The maximum number of ticks that a resource can live for before expiring.
Initial experiment values	agent-init	The number of agents to spawn at the start of the experiment.
	initial-weighting	The initial value of *info-weighting* for the starting agents.
Agent constants	vis-distance	The visual radius of the agents.
	move-distance	The distance an agent can move each tick.
	max-forage-time	The number of ticks an agent can be feeding, searching or following for before having to return to the roost.
	max-rest-time	The number of ticks an agent can stay at rest in the roost before having to go out foraging.
	max-agent-lifespan	The maximum number of ticks an agent can be alive for.
	max-agent-energy	An agent's *energy* can exceed this value but they must remain at rest in the roost until their *energy* is below this level. See section 5.4.7.
	birth-interval	The minimum number of ticks between births.
	birth-energy-ratio	The proportion of an agent's energy given to their offspring when they 'give birth'. Also dictates whether an agent has enough energy to produce offspring. See section 5.2.1.
	forage-cost	The amount of energy that it costs an agent to be away from the roost each tick.
	food-benefit	The amount of energy that an agent can gain from a resource while feeding.

5.4.1 Information acquisition versus information use

A distinction needs to be made between information acquisition and information use. Information acquisition is the act of gaining information about something, in our case resource locations. Information use is making a decision based on currently held information.

What we are considering in our model is the preference for one method of information acquisition over another. Information can be personally acquired through exploration of the environment. Once an individual spots a resource, that resource location becomes part of the agents personal information, as they know about it through their own observation. Information can be socially acquired by following another individual which one believes will take them to a resource. When the agent spots the resource, the resources location becomes personal information, not socially acquired information, as the agent has observed the resource.

One may consider that the agent has socially acquired information regarding the resource's location, prior to having spotted the resource, as it is through the behaviour of a conspecific that they believe there is a resource in the direction in which they are heading. However, in our model this information is never used, the location of a resource is never inferred, the agent faithfully follows. The use of information regarding resources, then, is entirely personal information use. If the agent has personal knowledge of resources then they utilise it. If they do not have personal resource information, they do not target resources that they 'believe' may exist through knowledge garnered from a conspecific.

5.4.2 Agent separation in the roost

As stated previously, the model does not include any separation between agents while they are at the roost. In a real colony, the roost may be spread over an area in which it is unrealistic to assume that all agents are visible to all other agents within the roost. We do not include this element in the model for two related reasons. Firstly, the sharing of information does not have to occur through the observation of conspecifics while they are at rest in the roost. There may be inadvertent social information presented or information communicated as the agent enters or departs from the roost which is visible to all members of the colony. An example of this is found in Guanay cormorants (*Phalacrocorax bougainvillii*) form rafts oriented in the direction of large groups of returning cormorants which are visible to any departing bird (Weimerskirch et al. 2010).

Secondly, there may be inadvertent social information that has a limited range of transmission, such as the regurgitation of meals for chicks signalling a successful forager, and therefore only informs local conspecifics. However, the resultant actions, such as following an individual when leaving the roost, may inform other conspecifics. The act of following could inform others that the followed individual is worth following.

5.4.3 Resource knowledge

Agents maintain a list of resources that they have seen. Resources are removed from this list if their expected location falls within the vision range of the agent after they have expired. The agent does not attach any further information to a resource in its memory other than its location. Therefore, it cannot make a decision on which resource is most likely to still have food, based on the amount of food that it held and the amount of time that has past since the last visit.

5.4.4 Following and targeting decisions

When making a decision regarding which agent to follow, individuals have 'perfect' awareness of whether an agent is leaving the roost *feeding* or not. The advantage to the follower of this ability is that they are guaranteed to be lead to a resource. It does not guarantee that the resource will still exist when the agent arrives; the followed agent or a 'third party' may have consumed all of the remaining food. This is a clear advantage relative to not being able to determine the purpose of a conspecific's foray which leaves the possibility of following a 'searcher' on a potentially fruitless outing. This simplification could be interpreted as analogous to the deliberate communication of information to conspecifics by those leaving the roost, as occurs in Guanay cormorants (*Phalacrocorax bougainvillii*) (Weimerskirch et al. 2010). Though one could also consider contexts under which information was inadvertently broadcast, as is seen in ospreys (Greene 1987).

Another simplification when deciding which agent to follow or which resource to target relates to making a decision when presented with many options. The agents in our model select one of the available options randomly rather than selecting the 'best' option. This is because of the ambiguity of what one should consider to be 'best'. The best resource location may be that which is closest, that which had the greatest magnitude of remaining resource when last visited, that with fewest conspecifics moving towards it or any combination of the above. The best agent could be that with the greatest energy level, the oldest, the one with the most/least followers etc. Further, what is considered best likely depends on the environment; in this case the resource patchiness and ephemerality. We could carry out experimentation to ascertain what constitutes best in each environment but random selection was considered suitable for the purposes of this model.

5.4.5 Perfect navigation

If an agent has a targeted destination, either a resource, agent to follow or roost to return to, that agent is able to navigate in a straight line towards the target. One may assume that it is unrealistic for animals to be able to navigate directly towards a distant target location. If an animal were to use landmarks to navigate, the path would be straight *between* the necessary landmarks but overall it would be rather winding. There are, however, many examples of species using Euclidean maps to travel directly to targeted locations, as discussed in section

2.4.

5.4.6 Forage and rest time limits

In order for the model to work in the patchiest of environments there is a need to 'force' agents to leave the roost after a period of rest. When socially acquiring information becomes greatly more beneficial to an agent than generating personal information by searching, those agents are less and less likely to leave the roost without another agent to follow. If all agents adopt this behaviour, as strictly they should, no agents will leave the roost to search for new resources and in turn, all the agents will starve. There are many mechanisms that one could imagine in nature that would force an individual to acquire information through searching, from increasing levels of hunger to a requirement to feed one's offspring regularly.

A limit is also placed on the amount of time an agent can spend foraging outside of the roost, whether searching, following or moving towards a known location. There are two reasons to do this. Firstly, if an agent is able to travel for an unlimited period, they can take advantage of the wrap-around nature of the model's environment, unless the environment is made infeasibly large or the cost of foraging is great enough to restrict the possible travel distance before death. Secondly, in order to add a modicum of realism to the agent's behaviour cycle. It is implausible in most species to forage without rest for an indefinite period of time (Lewis et al. 2004). As the roost is the sole place of rest for agents in this model, it is necessary for them to return to the roost after a period of foraging, whether successful or not.

5.4.7 Maximum energy threshold

In order to avoid agents eating 'unrealistic' amounts of food a threshold was put in place which stopped agents leaving the roost if their energy was 'too high'. There are examples in nature of animals eating more than is necessary in order to sustain themselves, but this is usually in preparation for a period of expected fasting such as hibernation. If the benefits and costs are properly calibrated for the experiments, then the waiting period should remain relatively short. This then may be considered analogous to the fact that in abundant environments individuals are able to spend more time on other activities, such as socialising, than solely on foraging (Monaghan et al. 1994).

Chapter 6

The effect of resource patchiness on information acquisition

In this chapter we apply our model to an exploration of the adaptivity of different information acquisition strategies -in environments of varying resource patchiness. We hypothesise that the patchier the resources within the environment, the more advantageous it is for an individual to acquire information socially rather than through exploration. If the total magnitude of food in two environments is identical but the relative patchiness is varied, the 'value' of information regarding the environment changes. In an environment in which one is guaranteed to discover a resource when leaving the roost, there is no pressure on an individual to adapt their information acquisition behaviour. However, in an environment in which it is unlikely that an individual will discover resources while foraging, there is an advantage to pooling information with a group, in order to spread the cost of foraging, as long as each resource location can sustain multiple agents. Our results lend weight to our hypothesis, showing that aggregation is advantageous to individuals when resource information is hard to discover alone.

6.1 Results

We ran the model sixteen times for a range of values of *num-resource-locations* between 1 and 100, over 500 generations at a time. The length of each generation was defined to be equal to the value of *birth-interval*. The *initial-weighting* of the agents was set to 0.5, meaning an equal preference for socially acquired and personal information. The lifetime of resources was not limited; they only expired through exhaustion of their food supply. The mean value of the *info-weighting* of all agents in the population was measured every ten ticks along with the population level.

Through preliminary experimentation, values for the various experimental variables, described in section 5.3, were decided upon. They were set to values that would maintain a

'reasonable' population level over a range of values of *num-resource-locations*. The values that were used can be found in appendix A.

During the runs in which *num-resource-locations* was set to a value below 20, no populations survived for the full 500 generations. Further runs were carried out in order to ascertain whether this was due to an inability of the populations information acquisition behaviour to adapt fast enough or whether the forage and return tactic wasn't suitable in the environment. These extra runs used an *initial-weighting* of 0.1 and values of *num-resource-locations* of 5, 10 and 15. None of the populations in these runs survived for 500 generations.

In order to quantify the probabilities of an agent discovering a resource when foraging a simple model was derived from the one described in chapter 5. The agent would start at the roost, go out searching using the same random search as described in the model, and after a number of ticks equal to *max-forage-time* the agent's success in finding a resource was recorded. This was measured for 1,000,000 agents over 1000 random permutations of resource locations. The environment varied in resource patchiness from 1 to 200 resources. The results, in figure 6.6, show that in the patchiest environment an agent $\sim 5\%$ chance of discovering a resource on a single outing. The number of resources each agent discovered was not measured, only their success in finding a resource.

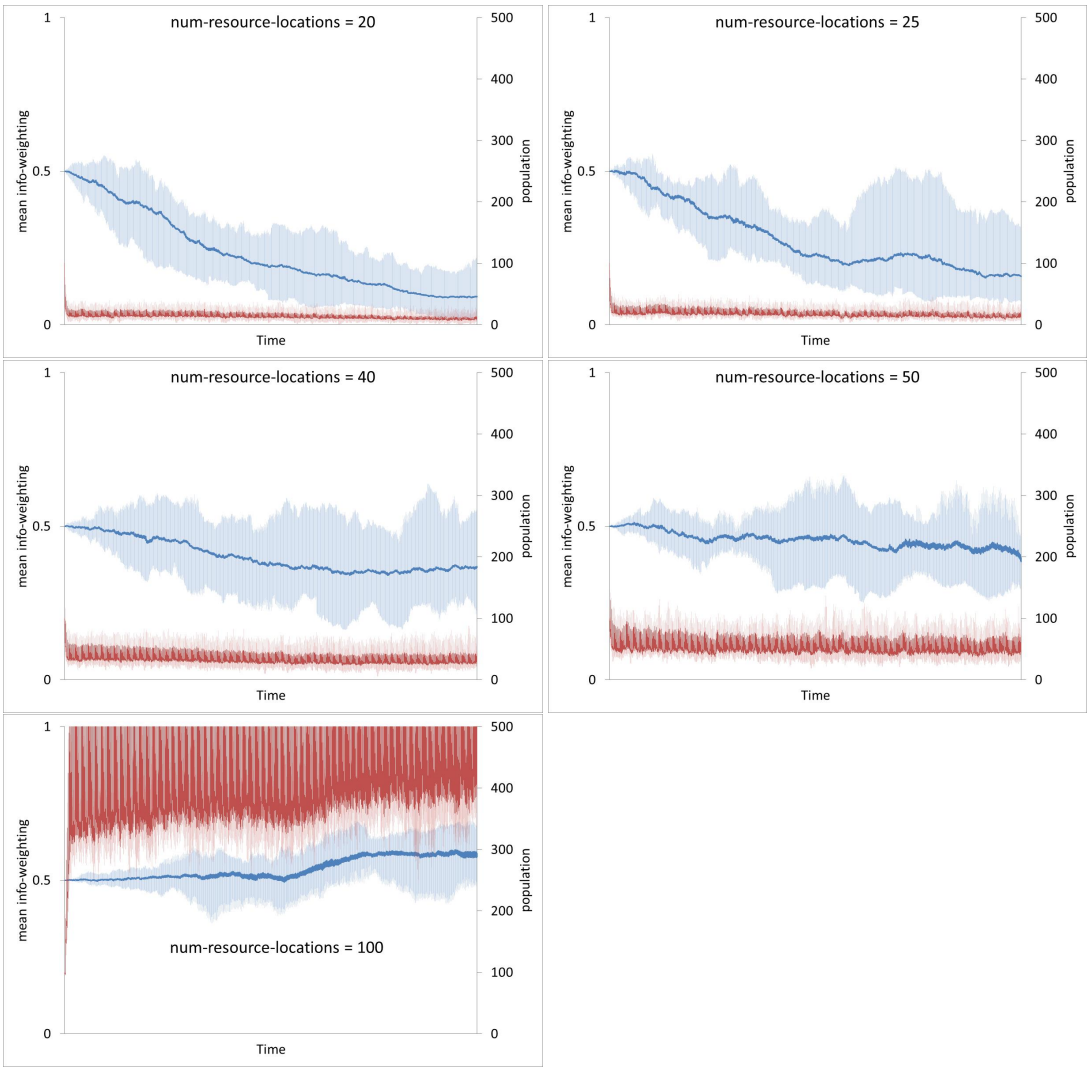


Figure 6.1: The mean *info-weighting* of the population of agents was measured every 10 ticks. The mean of the sixteen runs (blue line) shows that the *info-weighting* adapts over time to allow agents to preferentially use social acquisition of information (lower *info-weighting*) when resources are more patchily distributed (lower *num-resource-locations*). The blue shaded area around the blue line shows the range of mean *info-weighting* over the sixteen runs. The mean of the populations from the sixteen runs (red line) also varies with *num-resource-locations* as does the population range (red shaded area). Each experiment was run for 500 generations (2,000,000 ticks).

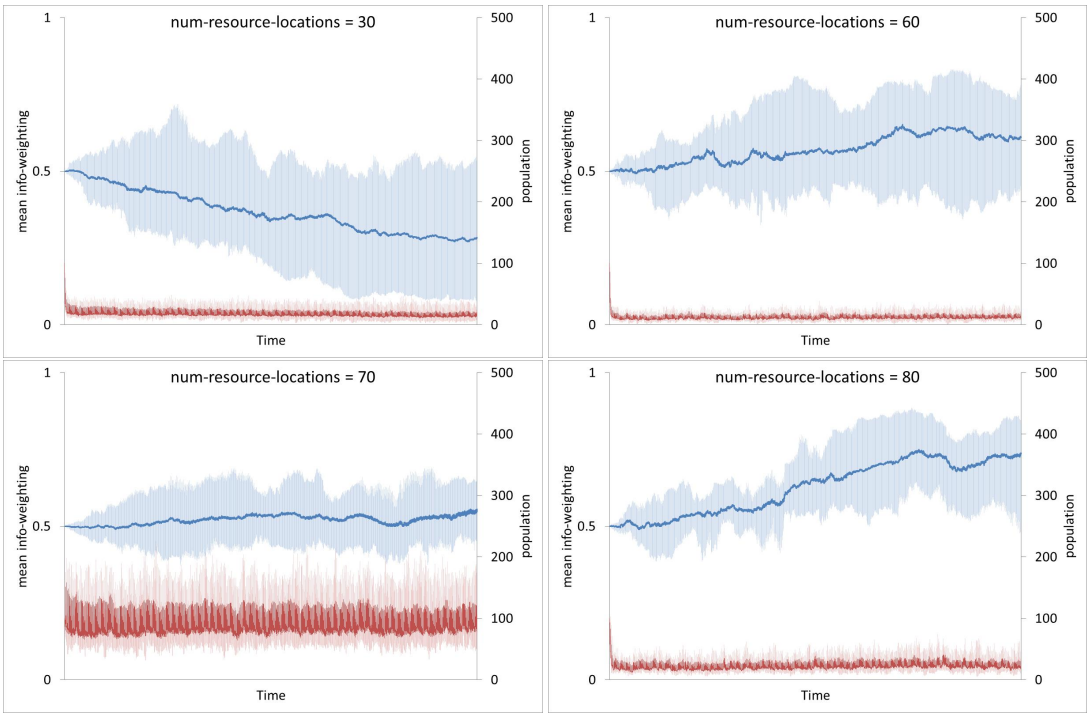


Figure 6.2: See description of figure 6.1. For the values of *num-resource-locations* in these graphs, the agents are not guaranteed a complete meal each time they find a resource.

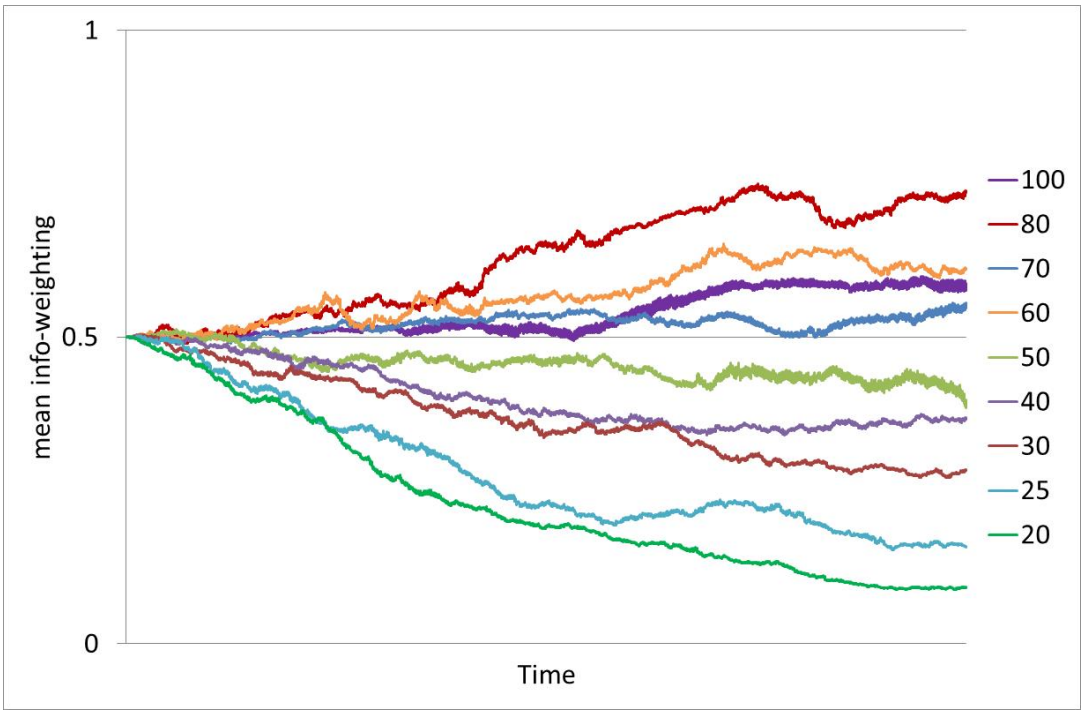


Figure 6.3: The mean *info-weighting*s over a range of values for *num-resource-locations*. The greater the patchiness the greater the trend towards a low *info-weighting* meaning a greater preference for social acquisition of information.

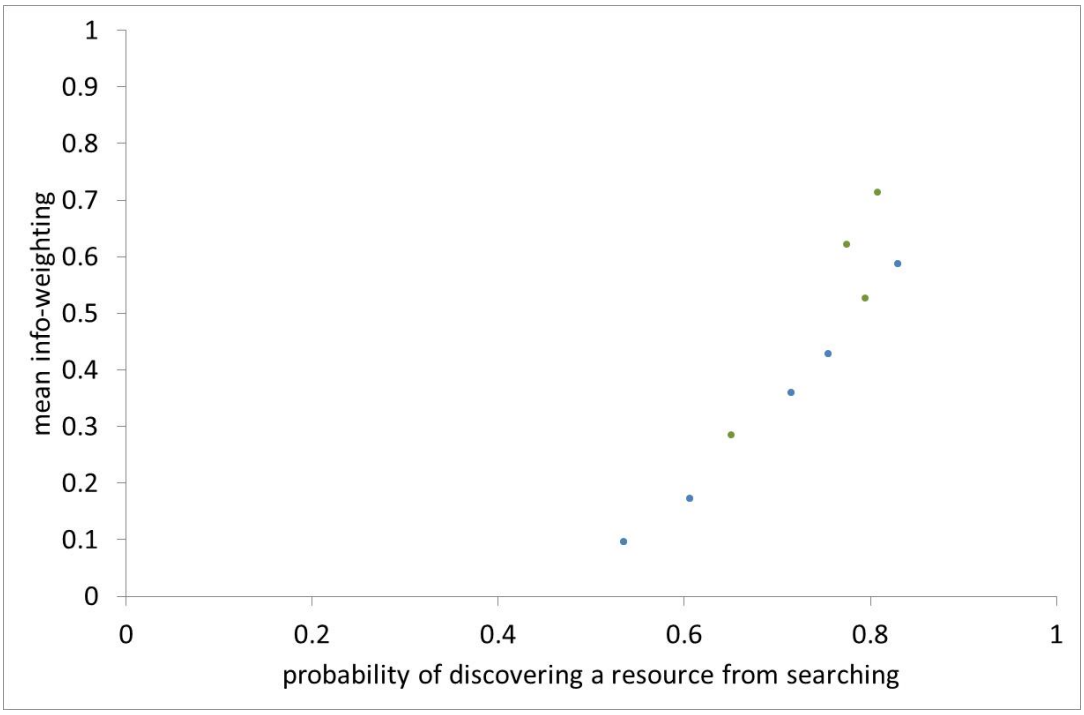


Figure 6.4: The trend in info-weighting showing a greater reliance on social acquisition of information as the probability of discovering resources diminishes. The blue data points are those in which the foraging agent will always receive a full meal when feeding, the green points are those in which this is not guaranteed. The mean info-weighting values are taken over the last 100 generations for experiments at each level of resource patchiness.

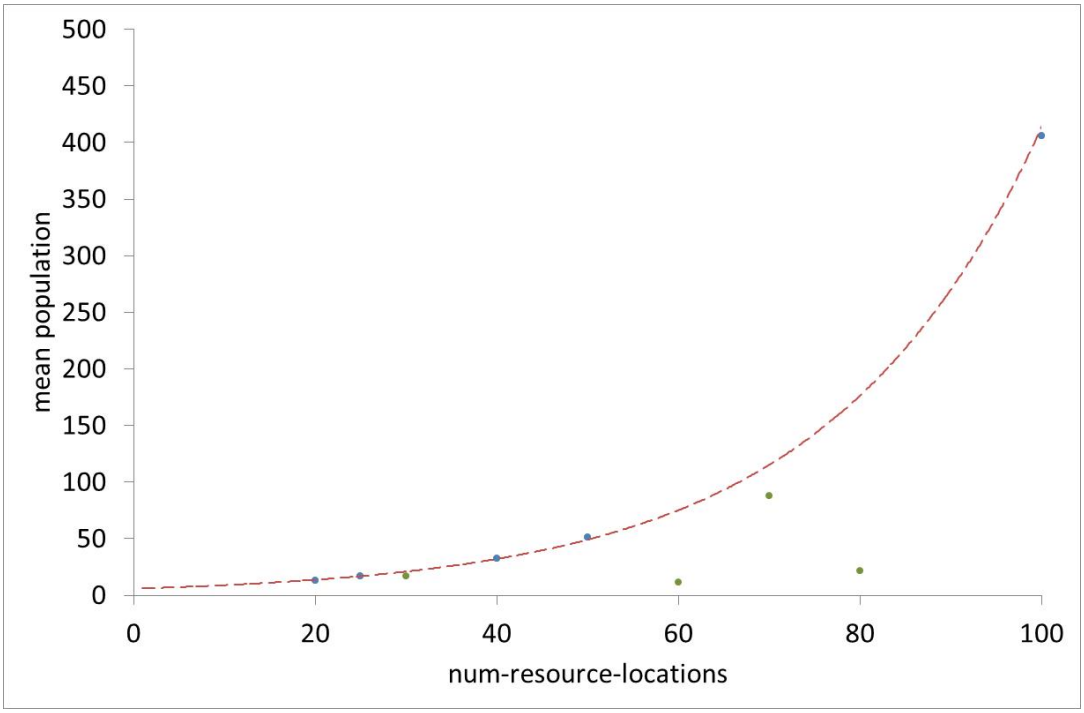


Figure 6.5: The mean population level over a range of environments with varying resource patchiness. As resources become less patchily distributed, and therefore easier to discover, the population level rises. For environments in which the maximum food held at a resource location is not divisible by the total amount that an agent can eat per trip, the population level falls, sometimes dramatically (green points). The red dashed line is an exponential trend-line, of the form $y = 5.8373e^{0.0426x}$ ($R^2 = 0.9995$), determined using the points where the magnitude of the resources in the environment is divisible by the benefit an agent gains from a resource per trip (blue points).

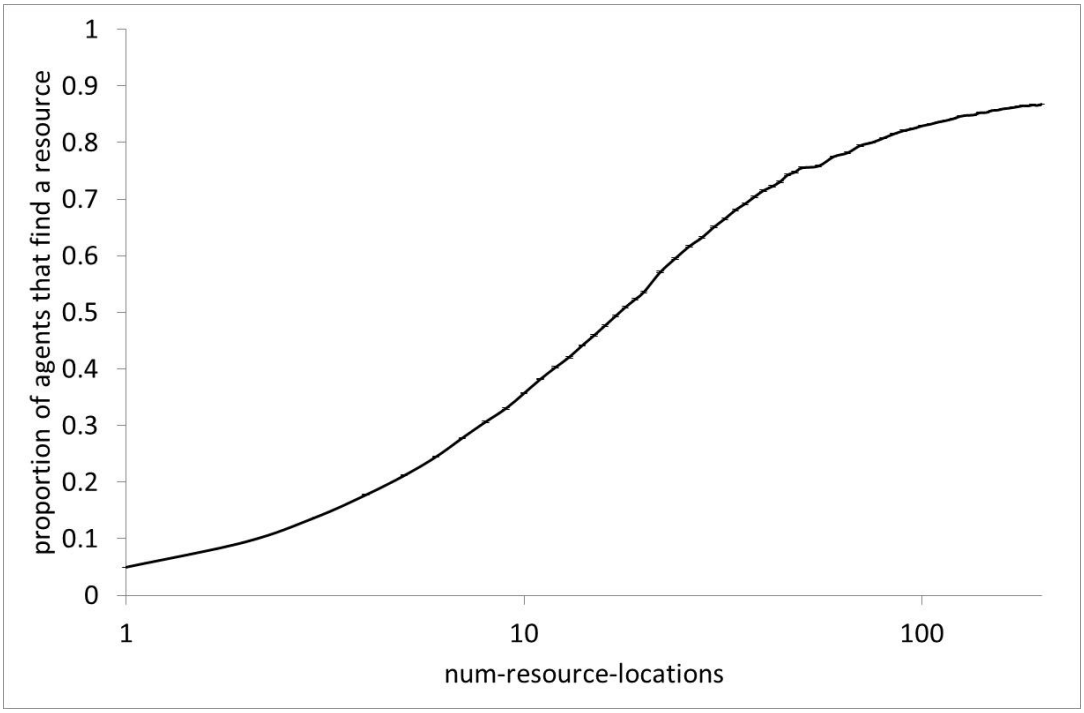


Figure 6.6: The proportion of agents that discover a resource when foraging on a single trip with varying number of resource locations. The error bars, though barely visible, show the standard error.

6.2 Analysis

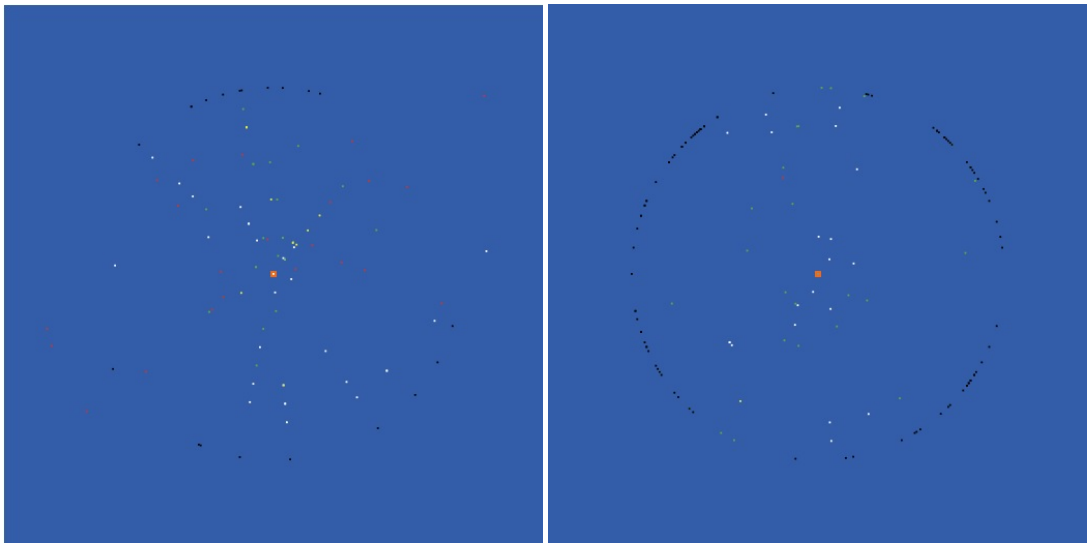
By varying resource patchiness within an environment we expected to see some adaptation in the way agents acquire information. We did not expect to see the variation in population levels that was shown. From these findings we can infer how resource patchiness may affect social structures in different environments.

6.2.1 Information acquisition strategy

As the number of resource locations diminishes, so too does the likelihood of an individual discovering resources, as shown in figure 6.6. Due to the energy cost associated with foraging, there is a limit to the number of unsuccessful expeditions an individual can make before dying. The sharing of information regarding resource locations with other agents allows individuals to access food that they have not had to find on their own. Sharing becomes more necessary as the likelihood of discovering one's own food diminishes. In patchier environments, this leads to a fitness advantage for those agents that socially acquire information to a greater extent than personally doing so.

As the likelihood of finding resources increases, the need to socially acquire information diminishes and a preference is shown for acquiring information through exploration. Two important attributes of the resources change as the number of resources increases. Firstly, the food held at each location diminishes, which has an impact on the likelihood of there being food remaining at a resource location on a return trip and when following another agent. This makes it beneficial for an individual to forage solitarily when the maximum food held at each location is suitably small. Secondly, the likelihood of other resources being visible from a resource location increases. This means that the possibility of following an individual and being left without food is reduced. Further, any form of excursion from the roost is likely to yield information on multiple resource locations. However, this information potentially has a shorter useful lifespan as it takes fewer visits to exhaust each resource location. As such, an agent is likely to have more 'junk' information in their memory than in more patchy environments.

In figure 6.3, we can see that the line for the mean info-weighting in the environment with 60 resource locations has a greater trend towards personal acquisition of information than in an environment with 70 resource locations. Further, the line for the environment with 100 resource locations is below the lines for both 60 and 80. If we look at figure 6.4 it becomes clear that it is actually the lines for 60 and 80 that seem to be high rather than those for 70 and 100 being low. The reason for this increased benefit from a personal information acquisition strategy can be seen in table 6.1. In environments in which the last meal before the expiration of a resource is small, it is beneficial to the individual to find resources alone. This is because there is an increased chance that, when following another agent to a resource location, the follower is left with a meal that does not return the energy expended on getting to the resource in the first place. However, when foraging alone, an individual is more likely to discover a new food patch and gain the full benefit that they



(a) num-resource-locations = 20 (b) num-resource-locations = 100

Figure 6.7: Images of the environments in which the agents act. The roost is shown at the centre (orange square) with a random distribution of resources (black circles).

would expect.

In order for an individual to be able to sustain itself within an environment, the attainable benefit needs to exceed the cost of foraging.

$$pb > c \tag{6.1}$$

where p is the probability of finding a resource, b is the benefit gained from a resource and c is the cost of foraging[1]. Using the values from figure 6.6, one can see that if an environment has only one resource in it, $p \approx 0.05$. As such, the benefit an agent can get from a resource would need to be twenty times the cost of foraging in order for a tactic of naive foraging to be sustainable.

We believe that an individual's mean energy level needs to be greater than c/p. This is necessary to ensure that there is a realistic chance that an individual will find a resource before dying. If an individual has to make an average of ten expeditions in order to benefit from a resource patch, they must have enough energy, on average, to sustain the cost of those expeditions.

One can see from equation 6.1 that an individual can affect its chances of survival in three ways: decrease the cost of foraging, increase the benefit that it can receive and increase its chance of finding resources. An agent could decrease the cost of foraging by, for example,

[1] c is likely to be a distribution of some form rather than a fixed value as there will evidently be times when an individual can feed at a resource closer to their current location then at other times. b may also not be constant if, for example, the individual feeds on a variety of resource types.

roosting closer to a resource location. However, this may not always be possible due to predation risk or the transient nature of resources. Increasing the attainable benefit from a resource is likely to be limited by the physiology of the animal; only so much can be eaten in one 'sitting' or only a certain amount of food can be carried back to the roost. Over time species will specialise to draw maximum benefit from the foods within their environment.

Improving the chances of discovering resources can be accomplished, as we have seen, by sharing information. However, sharing information is not always necessary and in some cases can be detrimental. Therefore, an individual's preference for the use of different forms of information should be determined by the relative probability that it will successfully lead to resources.

$$p = wp_p + (1 - w)p_s$$

$$(wp_p + (1 - w)p_s)b > c \tag{6.2}$$

where $0 \leq w \leq 1$ is the individuals preference for personally acquiring information, p_p is the probability of finding a resource when searching alone and p_s is the probability of finding a resource by socially acquiring information. However, when the likelihood of socially acquired and personal information leading to successful foraging is equal, personal information should be preferred as there is a reduction in competition at resource locations. Therefore, we should not consider p_p and p_s as the probabilities of *finding* a resource, either personally or socially. Rather, they should be the probability of receiving benefit b when using using the respective forms of information acquisition. Resource patchiness is certainly a factor in these probabilities but we must also consider competition from conspecifics.

It must be made clear that when we talk about agents adapting their strategy, this is a process that occurs over multiple generations. The information acquisition strategy of any individual agent is fixed from birth. It is through 'genetic' variation in offspring that the strategy of the agents changes and through selection driven by energy requirements that one strategy out performs another.

6.2.2 Population levels

As can be seen in figure 6.5, the average population level varies with patchiness. The maximum amount of food within the environment remains the same through all experiments. As resources are exhausted, they are replaced with new resources at a new location. If a resource only holds enough food for a single trip form a single agent, it will be exhausted and regrown in a single tick, maintaining the maximum level of resource within the environment. At the other end of the scale, if a single resource held all of the environment's food, the total food in the environment will be reduced to an amount that can sustain only a single agent.

The number of unique resource locations discovered by the group is very important. In very patchy environments, for example *num-resource-locations* = 20, if all agents go searching

Table 6.1: The amount of food left at each resource location for the last 'meal' when the total amount of food in the environment is equal to 20,000 and agents eat 100 resource at a time.

num-resource-locations	resource magnitude mod 100
30	66.67
60	33.33
70	85.71
80	50

for resources, $\sim 54\%$ will make a discovery, as shown in figure 6.6. In our experiments, when *num-resource-locations* $= 20$, each resource held 1000 food and each agent would eat 100 of it on each trip. In this environment the stable population level was ~ 13 agents, as shown in figure 6.5. If only one resource location was found, 13×0.54 agents will eat some food on the first trip, reducing the food held at the resource to $(1000 - ((13 \times 0.54) \times 100)) \approx 300$, while all agents will experience a cost. On the return trip there will only be enough food for three agents, though ~ 7 plus however many choose to follow will attempt to feed there. If, however, two resource location were discovered, the amount of food known about after the initial expedition would be ~ 1300, enough to feed all returning individuals and followers. Although, depending on how many agents attempt to feed at each resource location, some agents may still return without any benefit after two expeditions.

Figure 6.5 shows that, in situations in which the amount of food held at a resource is not divisible by the benefit an agent can gain from that resource per trip, the population level falls below he trend-line. When *num-resource-locations* is equal to 60 and 80, it is vastly below where one would expect it to be. Table 6.1 shows the amount of food held by each resource modulo the amount an agent removes per trip. In conjunction with figure 6.5, it becomes clear that in environments in which the last 'meal' available from a resource is particularly small, the population suffers. With the values that we used in our experiments, the cost to an agent of successfully foraging is ~ 60 while the benefit gained is 100. Through further use of our model, with *num-resource-locations* ranging from 200 to 2000, we could determine the minimum magnitude of food held by resources necessary to sustain a population. One would expect it to be higher than 60 due to the effects of competition at food patches and the fact that an individual has, at most, a $\sim 90\%$ of discovering a resource location when searching.

6.2.3 Social structure

One can see that the adaptivity of socially acquiring information is related to the patchiness of resources in the environment. In patchy environments, individuals that are able to acquire social information will out compete those that are not able to do so. In order to have the option of socially acquiring information, individuals need to be part of a social structure that allows them to observe or interact with each other. Colonies are one such social structure and therefore the need to acquire information socially may have influenced

its evolution.

However, in less patchy environments, where socially acquiring information is not beneficial, this can no longer be considered a pressure to aggregate. In fact, the increased resource competition would penalise grouping behaviour. As such, in the less patchy environments a colonial social structure is unlikely to arise without other pressures to aggregate.

6.3 Conclusion

We aimed to show that the patchiness of resources within an environment effects the method of information acquisition that is most beneficial for individuals to use. A model was built in which the preference agents give to different information acquisition techniques is allowed to vary from generation to generation. Over a range of environments, in which the number of resource locations was varied, a trend was observed that agrees with our hypothesis. The experiments also show how dramatically the population is affected when there is a chance of only receiving a partial benefit from a resource location.

Chapter 7

The effect of resource ephemerality on information use

In this chapter, we apply our model to an exploration of the adaptivity of different information acquisition strategies in environments of varying resource ephemerality. We hypothesise that in environments where resources last for only short periods of time, it is advantageous for conspecifics to socially acquire information regarding resource locations and therefore advantageous for them to aggregate. In an environment in which resources remain static for long periods of time, one is able to return many times and therefore rarely needs to search for new resources. However, in an environment in which resources remain at a location temporarily, individuals will have to search more regularly for new resources. Therefore, there is an advantage to pooling information with a group in order to spread the cost of foraging. Thus, the relative importance given to socially acquired or personal information when making a decision will depend on the ephemerality of resources within their environment.

Our experimentation lends weight to our hypothesis but highlights the fact that even sharing information cannot help a group when the resources within the environment are both very patchy and ephemeral. However, due to an inconsistency in our model, further investigation is needed in order to fully explain the continued trend towards a social information acquisition strategy, when any form of information is seemingly irrelevant.

7.1 Results

We ran the model eight times for a range of values of *max-resource-lifetime*, with values of *num-resource-locations* from 5 to 60, for 500 generations at a time. The other experimental variables were set to the same values as those used in the previous experiment, see appendix A. The mean value of the *info-weighting* of all agents in the population was measured every ten ticks along with the population level.

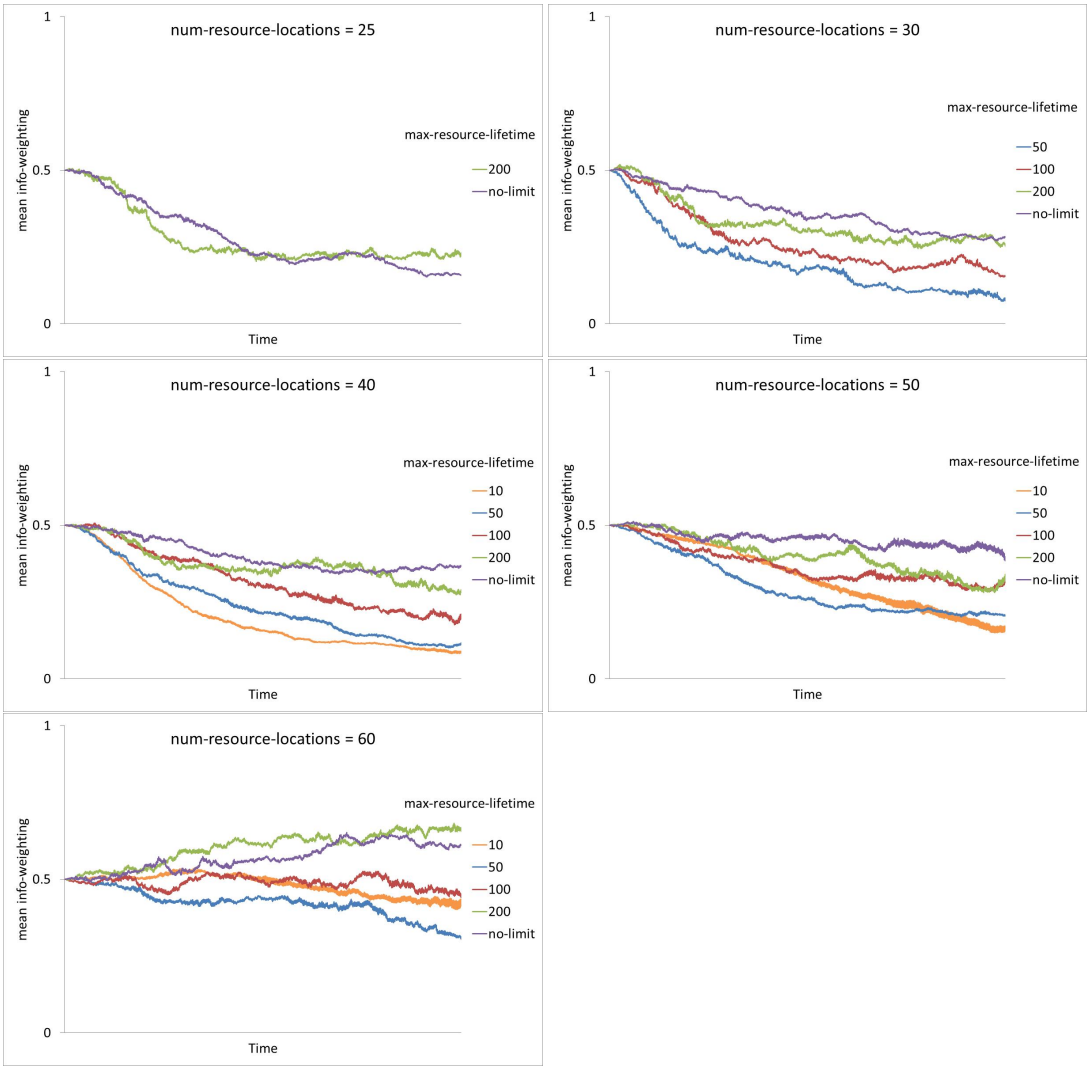


Figure 7.1: The mean *info-weighting* of the population of agents was measured over a variety of levels of resource ephemerality (*max-resource-lifetime*). This was repeated for a number of levels of environment patchiness (*num-resource-locations*). Since it takes at least 20 units of time to return to a resource location after first feeding at it, information about resources is redundant when the resource lifetime is set to 10.

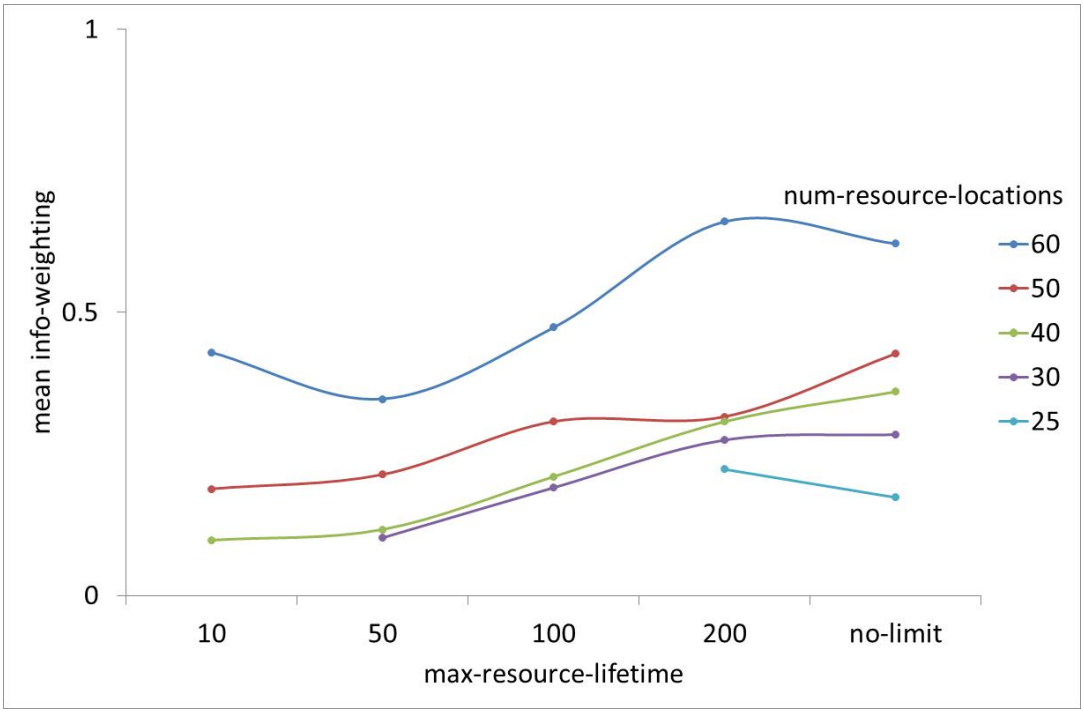


Figure 7.2: The trend in info-weighting as resource lifetime is varied, for a variety of levels of patchiness. As shown in chapter 6, the less likely that it is for an agent to discover a resource by searching, the more the agent relies on socially acquiring information. Here we see that as the lifetime of resources in the environment increases, the social acquisition of information diminishes.

In environments in which the number of resource locations was below 30, no populations survived for 500 generations, with the exception of *num-resource-locations* = 25 and *max-resource-lifetime* = 200. When *num-resource-locations* = 30 and *max-resource-lifetime* = 10 no populations survived for 500 generations.

Results from the previous experiment, see chapter 6, were included in the graphs to show the information acquisition trend when there was no limit placed on the lifetime of resources.

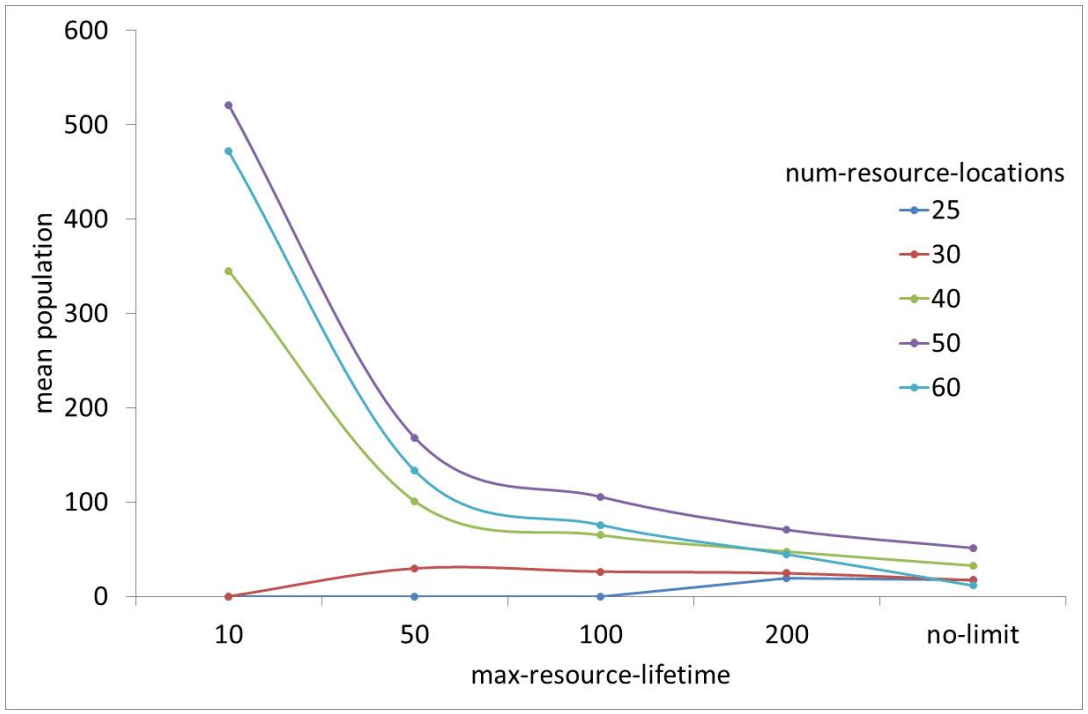


Figure 7.3: The mean population level for each of a variety of resource emphemerality and patchiness levels. The points at which mean population level is equal to 0 are from experiments in which the population died out before 500 generations had been born.

7.2 Analysis

By varying the ephemerality of resources in our environment we were able to explore how individuals in a colony might adapt their information acquisition strategy. We also see that there is a dramatic effect on the sustainable population level when the lifetime of resources changes.

7.2.1 Information acquisition preference

One can see from figures 7.1 and 7.2 that the shorter the lifespan of resources within the environment, the greater the benefit provided by favouring social acquisition of information. However, when resources are very patchy and ephemeral, the benefits of socially acquiring information cannot outweigh the costs of foraging in those environments.

When *max-resource-lifetime* = 10, all known information is redundant. This is because, after an agent has discovered a resource for the first time, it will take them 10 ticks to return the the roost and, assuming they attempt to return to the resource patch immediately, another 10 ticks to get back. Therefore the resource is guaranteed to have expired before they are able to return to it. In less patchy environments this is less costly to the agents as there is a greater chance that other resource patches will be visible from the one they were returning to. However, in patchier environments, a trip to an expired resource location is unlikely to lead to the discovery of a new resource and therefore there is a decreased chance of eating but the same cost is sustained. This is likely to explain why populations were unable to survive in the tests with lower numbers of resources and resource lifetimes.

Further, when *max-resource-lifetime* = 10, socially acquiring information is not guaranteed to lead an individual to a resource. In fact the opposite is true, since the followed agent will be heading towards an expired resource location. As such, the trend towards using a social information acquisition strategy, when resources are extremely ephemeral, cannot be due to a reduction in foraging costs from group search.

One potential reason for this may be due to a flaw in the way the model randomly locates new resources. In order to randomly locate the resource at a given radius from the roost a random x coordinate is chosen within a range bounded by $\pm radius$. From this a y coordinate is generated using $y = \sqrt{radius^2 - x^2}$, negating it with a probability of 0.5 in order to place the resource on a circle rather than an arc. However, this method has the unintended effect of 'favouring' locations closer to the north and south poles of the circle, as shown in figure 7.4. Since, when searching for food, the agents leave the roost in a random direction, they have an equal chance of heading east/west and north/south. If, however, the agent chooses to follow another agent they are more likely to be lead north/south since that is where agents are more likely to discover resources. As such, agents are more likely to find a resource with food remaining, when following, despite the increased competition. Although this trend in behaviour may be the result of an error in how resources are located, it does show that the agents are able to adapt their behaviour to take advantage of patterns

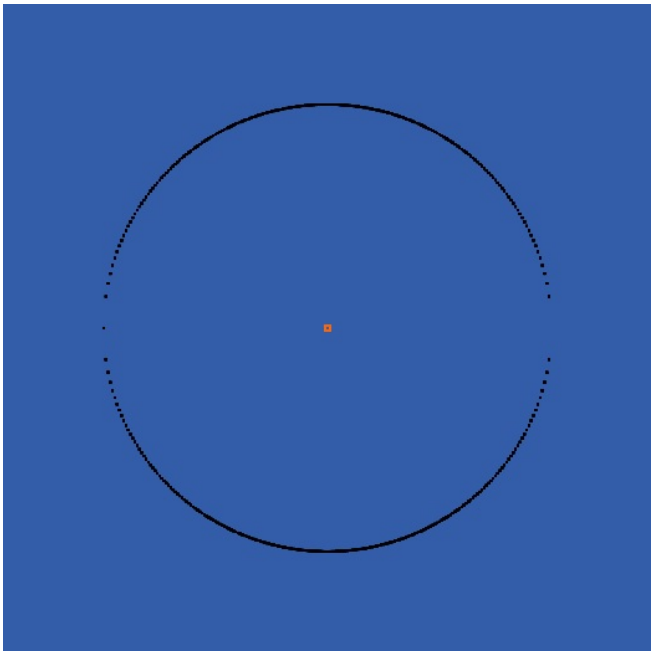


Figure 7.4: An image of the environment with 5000 resource locations. One can see the 'bias' of the random location method towards the north and south poles.

in their environment.

7.2.2 Population level

As can be seen in figure 7.3, in the less patchy environments, the population level increases as the resources' lifetimes decrease. Even in the patchier environments, there is a slight increase in population level as resources become more ephemeral. However, in those patchier environments, populations are unable to sustain themselves when resources become too ephemeral. This is because, in the patchiest of environments, the decreased probability of finding resources is countered by the ability to return multiple times to a known resource. If the resource expires before the agent has been able to take full advantage of the ability to return, foraging becomes more costly until it is unsustainable. Even if an agent acquires information socially, they will suffer the same cost of travelling to an expired resource location without much chance of seeing another resource from their targeted location. Therefore, social acquisition of information does not shelter the agent from the most ephemeral environments.

In contrast, the less patchy environments do not punish those travelling to expired resource locations due to the increased likelihood of being able to see other resource from the targeted location. In fact, the renewal of resources is beneficial when the chances of discovering them are high enough. If a group of agents are all moving towards the same area, in order to feed,

there will be competition for resources. When resources expire only when the food they hold has been exhausted, there is a greater chance of the resources in an area not holding enough resource for the entire feeding group due to previous feeding trips. However, if the resources are regularly regrown, there is a reduced chance that a group of agents will reach a location that has been severely depleted by previous trips. This means that ephemerality is beneficial in environments in which it is not too hard to discover new resources.

7.3 Conclusion

It was proposed that ephemerality of resources would influence the information acquisition strategy used by individuals within a colony. We explored the changes in the information acquisition strategy over a range of levels of ephemerality and for a number of different levels of resource patchiness. Our model shows that it is beneficial for individuals to give greater preference to social acquisition of information as the ephemerality of resources increases. However, this result may be due to our method for randomly locating resources. We showed that even acquiring information socially doesn't help a group when in very patchy and ephemeral environments.

Chapter 8

Conclusion & future work

In this chapter we discuss some of the problems we came across when building our model. We go on to consider extensions to our model and further work that could be carried out with regards to what we have achieved.

8.1 Discussion

Our model went through many iterations in order to remove unexpected and unwanted environmental factors and refine the behaviour of the agents.

8.1.1 Locating resources

In previous versions of our model, resources were located randomly in a 200×200 square centred on the roost. Though this seems like a more natural representation of the environment in which a colonial species might find itself, it introduced an extra, unexpected factor. The population level of agents in environments in which resources were easy to discover was lower than in the patchier environments. As each resource location in the less patchy environments held less food, they would be exhausted quickly and the closer the resource was to the roost, the faster it would be depleted. This lead to the average distance to resource locations in the less patchy environments being greater than in the patchier ones. Further, new resources that happened to grow close to the roost in the patchiest of environments would provide a food bonanza, being able to feed many agents with minimal travel cost. In order to remove this effect from the environment we implemented a set distance from the roost to resources, resulting in a ring of resources around the roost. This meant that the probability of discovering food, and not the travel cost, was varied when the environment was.

8.1.2 Information acquisition and information use

As mentioned in section 5.4.1, our model makes the distinction between an agent's information acquisition and information use strategies. In initial versions of the model the two were conflated. If an agent chose to 'use' personal information, they would move to a resource location if they knew of one and if not, they would search for one. If an agent chose to use socially acquired information they would attempt to find a suitable agent to follow and if none existed they would remain in the roost. This ignored the statement by Richner & Heeb (1995, pg. 4) that "after a visit to the colony, the successful foragers return to the previously discovered feeding site", instead making the assumption that successful foragers would only return to known resources if they chose to use their personal information. The results produced the same trends, that the patchier the environment the greater the reliance on socially acquired information. However, as one would expect, for experiments with equal levels of patchiness the agents that conflated information acquisition and use had a greater preference for personal information in order to allow them to take advantage of known resources. Further, the agents in the experiments with separated information use and acquisition were able to sustain populations in the patchiest environments, of which the other agents were incapable.

8.2 Future work

During our research and experimentation, several further areas to explore became evident. Some of them involve simple extensions to our current model to explore inconsistencies in our results or to add extra dimensions of interest.

Fitting the variables that define our agents' abilities, such as vision distance or maximum foraging time, to those of real colonial species would allow our model to make predications regarding the behaviour and sustainability of that species in differing environments. Confirmation of those predictions, through empirical study, would lend weight to the validity of the model.

8.2.1 Inaccurate information transfer

The model, as described in chapter 5, enables the agents to socially acquire information with perfect accuracy. The agent only chooses to follow agents that are known to be heading towards a resource location. However, information is not usually transferred perfectly, not even when it is deliberately communicated. It would be interesting to investigate how the accuracy of information that an individual is able to socially acquire, impacts the preference given to a social acquisition strategy.

8.2.2 The successful forager problem

As described in section 2.5.1, one of the issues remaining with the information centre hypothesis is finding a valid motivation for a successful forager to return to the roost.

Roost separation & kin selection

We claimed in section 5.4.2 that socially acquirable information in colonies is visible to all members of the colony. However, there are likely to be cases where information is only transferred over a limited range or the accuracy of social information can be improved by shorter range observation. If we consider the case of birds in a breeding colony, the feeding of chicks with a regurgitated meal is likely to inform local conspecifics of the individual's recent foraging success. Further, the size of the individual's chicks will be an indicator of their foraging prowess, though this is unlikely to be a factor when success in foraging is not due to the skill of the forager. As such, an interesting extension to the current model would be to add a spatial distribution of agents when resting in the roost.

One of the mechanisms described by Richner & Heeb (1995) to explain why a successful forager might return to the roost uses a kin selection model. If sharing information with members of the colony increases a forager's inclusive fitness then such a behaviour will be adaptive. Čače & Bryson (2007) showed that the viscosity of a population has an impact on the adaptiveness of altruistic behaviour. The more viscous the population, the more likely it is that one's altruistic act will benefit their kin and therefore increase their inclusive fitness.

Predation pressure

One of the alternatives, suggested by Richner & Heeb (1995), to the ICH is the recruitment centre hypothesis, as described in section 2.5.3. Recruiting conspecifics, or being recruited, to a food patch can occur for several reasons from being able to kill larger prey to fighting off other groups or individuals. Predation avoidance and detection is also thought to be a reason to forage in groups due to the ability for individuals to reduce the amount of time they must devote to vigilance rather than feeding as well as reducing the probability of being targeted by a predator. Richner & Heeb (1995) propose that recruiting individuals may explain why a successful forager would return to the roost.

Previous work by Jenks (2009) showed how predation pressures can affect social foraging behaviour using agent-based modelling. Agents form foraging groups due to the increased risk of predation when foraging alone. If one were to use this predation risk model to provide an impetus for successful foragers to return to the roost, the pay off given to agents that 'protect' the successful foragers is the benefit gained from socially acquiring information.

8.3 Conclusion

We set out to explore how the environment in which individuals live might affect the way that they acquire information. The reason for undertaking this exercise was to explore the circumstances under which aggregation, for the purposes of information sharing, might arise. We hoped that our results would help to define a range of environments in which theories of aggregation that rely on information transfer, such as the information centre hypothesis, are viable.

We explored how variation in the patchiness and ephemerality of resources has an effect on the benefits of relying more on socially acquiring information rather than personally acquired information and vice-versa. As expected, when resources become more difficult to discover individually, it is advantageous for individuals to try and acquire information from others in their group. Further, due to increased competition, in environments in which one can discover food more easily, it is advantageous for individuals to forage alone. Our results from experimenting with the ephemerality of resource locations showed the same expected trend; the shorter lived the resource, the more beneficial it was for individuals to socially acquire information. However, our results also showed that even when it was impossible for a knowledgeable agent to return to a food patch, and therefore impossible to lead conspecifics to one, there was still selective pressure towards socially acquiring information. We believe that actually the agents were taking advantage of a bias in the way resources were located.

Our experimentation did not look at the current, major issue with the information centre hypothesis, the successful forager problem. We believe, however, that the model we have built provides a foundation that can be expanded upon to explore mechanisms that propound to resolve this issue.

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Appendix A

Experimental variables — values used

Table A.1: The values used for the experimental variables.

Variable	Value
total-resource	20,000
num-resource-locations	variable
max-resource-lifetime	variable
agent-init	100
initial-weighting	0.5, unless stated otherwise.
vis-distance	12
move-distance	10
max-forage-time	20
max-rest-time	20
max-agent-lifespan	9,000
max-agent-energy	500
birth-interval	4,000
birth-energy-ratio	0.66
forage-cost	2
food-benefit	100